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CONTENTS

PAGE

No. 1.—THE AMPHIBIANS OF THE SOLOMON ISLANDS. By Walter C. Brown. (8 plates.) August, 1952 . . . 1

No. 2.—REVISION OF THE ANT GENUS SERRASTRUMA. By William L. Brown, Jr. August, 1952 65

No. 3.—THE CARABID BEETLES OF NEW GUINEA. Part 2. The Agonini. By P. J. Darlington, Jr. (4 plates.) August, 1952 87

No. 4.—REVISION OF THE SPECIES CURRENTLY REFERRED TO ALEPOCEPHALUS, HALISAURICEPS, BATHYTROCTES AND BAJACALIFORNIA, WITH INTRODUCTION OF TWO NEW GENERA. By A. E. Parr. September, 1952 . . . 253

No. 5.—GEOGRAPHIC VARIATION IN THE RED-EYED TOWHEE OF THE EASTERN UNITED STATES. By J. C. Dickinson, Jr. October, 1952 271

No. 6.—CYATHASPID FISHES FROM THE VERNON SHALE OF NEW YORK. By R. H. Flower and R. Wayland-Smith. (8 plates.) October, 1952 353

No. 7.—NOTES ON SOME PETRELS OF THE NORTH PACIFIC. By Oliver L. Austin, Jr. November, 1952 389

No. 8.—AIRPLANE OBSERVATIONS OF HOMING PIGEONS. By Donald R. Griffin. December, 1952 409

No. 9.—THE APSEUDID CHELIFERA OF THE EASTERN TROPICAL AND NORTH TEMPERATE PACIFIC OCEAN. By Robert James Menzies. February, 1953 441

No. 10.—ON THE EARTHWORMS OF THE ARNOLD ARBORETUM, BOSTON. By G. E. Gates. February, 1953 . . . 497

No. 11.—A NEW FOSSIL TORTOISE FROM THE THOMAS FARM MIOCENE OF FLORIDA. By Ernest Williams. February 1953 535

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THE AMPHIBIANS OF THE SOLOMON ISLANDS

By Walter C. Brown

With Eight Plates

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
August, 1952

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No. 1.— *The Amphibians of the Solomon Islands*[1]

By Walter C. Brown

CONTENTS

Page
INTRODUCTION 4
  Acknowledgments 5
  Gazetteer of Solomons collecting stations 6
  List of nomenclatural changes 7
  List of amphibians of the Solomon Islands with an index to species . . . 7
  List of extralimital amphibians discussed in the text 8
  Notes on the geology and geography of the Solomon Islands 8
  Nature and distribution of the amphibian fauna 11
DISTRIBUTIONAL CHART SHOWING KNOWN RANGES OF THE SPECIES WITHIN THE SOLOMONS 14
  Treatment of data in the systematic section 16
SYSTEMATIC DISCUSSION 17
  Key to families 17
  Bufonidae 17
    Genus *Bufo* 17
  Hylidae 18
    Genus *Hyla* 18
  Ranidae 23
    Genus *Batrachylodes* 23
    Genus *Ceratobatrachus* 28
    Genus *Cornufer* 31
    Genus *Discodeles* 35
    Genus *Palmatorappia* 44
    Genus *Platymantis* 45
    Genus *Rana* 55
BIBLIOGRAPHY 61
PLATES 1-8

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[1] Submitted in partial fulfillment of the requirement for the degree of Doctor of Philosophy in the Department of Biology, Stanford University, April, 1950.

INTRODUCTION

The first general account of the herpetofauna of the Solomon Islands was that of Boulenger (1886). In that account he gave detailed descriptions of the nine species of amphibians and the nineteen species of reptiles then known to inhabit this archipelago. At that time all of these amphibians and five species of the reptiles were known only from the Solomons.

In the second general study of this herpetofauna (Kinghorn, 1928) the number of species of amphibians listed was still nine while the number of reptiles had increased to thirty-five. The amphibian list differed, however, from that of Boulenger in that two of the species on his list had been placed in synonymy and two species which had been discovered in the intervening period were included.

Since 1928, six species and subspecies of amphibians, including those described by the present writer, have been recognized from the Solomons; two earlier described species have been revived; and one species from the Americas has been introduced. Thus, eighteen species and subspecies are now known.

This growing list of species, which are recorded in numerous, scattered papers, as well as the recent collections made by various men at the time of the occupation of these islands by the United States military forces, make timely a preliminary revision and summary of our knowledge of this part of the fauna of this zoogeographically important archipelago.

A total of 1044 amphibian specimens from the Solomons have been examined during the course of the present study.[1] In some instances the available material has shown the existence of subspecific populations within the Archipelago. In other instances suspected populations are represented by inadequate samples and no prediction as to their racial distinctness is made at this time.

The number of new forms discovered in recent collections, in correlation with our relatively limited knowledge of the interior portions of many of the islands, suggests that additional new species may well remain to be discovered. Certainly the opposite conjecture (Boulenger, 1888a and Barbour, 1921) that the herpetofauna of the Solomons was probably well known has not been substantiated.

This study, as well as the author's work with the herpetofaunas of other Pacific island groups, has shown the great difficulty of determining phylogenetic affinities and the most probable distributional paths. There is a great need of generic and family revisions in both the amphibian and reptilian faunas which would include all the forms known to inhabit any part of this island region and also their Australian and Asiatic relatives.

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[1] Eighty-four of these are not listed in this paper because they are to be reported by other workers.

Acknowledgments

An expression of thanks is due especially to Dr. George S. Myers of the Natural History Museum at Stanford University and Mr. Arthur Loveridge of the Museum of Comparative Zoology at Harvard College who have assisted most generously with both time and knowledge. I also wish to thank Dr. H. W. Parker of the British Museum for making available to me unpublished distributional tables of the herpetofauna of these islands. I am also deeply indebted to the following persons who have permitted me unlimited use of the Solomon Islands collections deposited at the institutions with which they are associated: Mr. Charles M. Bogert of the American Museum of Natural History, New York; Dr. Doris M. Cochran of the United States National Museum, Washington, D. C.; Mr. Joseph R. Slevin of the California Academy of Sciences, San Francisco; Dr. Lawrence M. Klauber of San Diego, California; Dr. Robert C. Stebbins of the Museum of Vertebrate Zoology, University of California, Berkeley. Thanks are due Dr. Robert Mertens of Senckenberg Museum, Germany; Mr. Karl P. Schmidt and Mr. Clifford H. Pope of the Chicago Natural History Museum and Dr. Vasco M. Tanner of Brigham Young University for the loan of critical material whenever it was needed, even though their Solomon Islands collections were being studied by themselves or other workers at this time. I am also indebted to Mr. Walter L. Necker of Chicago who was so kind as to give his assent to the use of some of his material deposited in the National Museum.

Finally, I wish to acknowledge my indebtedness to Miss Virginia Field for some of the drawings of *Batrachylodes* and *Hyla thesaurensis*, Mr. William Theiss for the full-figure drawings of *Batrachylodes trossulus* and *Platymantis myersi* and especially to Miss Jean Allred for the preparation of all the other drawings illustrating the text and to Mrs. Charles S. Richards and my wife, Jeanette S. Brown, who patiently typed and corrected the manuscript.

The field work which provided the collections directly used in this study was conducted by: William M. Mann for the Museum of Comparative Zoology, 1916; J. A. Kusche for the California Academy of Sciences, 1921; Rollo H. Beck for the American Museum of Natural History, 1920–1928; Karl P. Schmidt for the Chicago Natural History Museum, 1929; Maurice Willows, Jr. for the California Academy of

Sciences, 1933; Lowell Adams for the Museum of Vertebrate Zoology, 1944; D. Eldon Beck for Brigham Young University, 1944–1945; John Chattin for the Museum of Vertebrate Zoology, 1944; J. A. Gray for the Museum of Vertebrate Zoology, 1944; J. P. Heath for the Natural History Museum of Stanford University, 1944; L. W. Jarcho for the Museum of Comparative Zoology, 1943–1944; D. H. Johnson for the United States National Museum, 1944; Walter L. Necker for the United States National Museum, 1944; R. C. Pendleton for Brigham Young University, 1944; Ernest Reimschissel for Brigham Young University, 1944; Charles G. Sibley for the Museum of Vertebrate Zoology, 1944.

Gazetteer of Solomons Collecting Stations

In the following list of localities, whether small, generally unnamed islands on the ordinarily available maps or known collecting stations on the larger islands, latitude and longitude as well as synonyms occurring in the literature are given. Latitudes and longitudes were determined largely from tables in the United States Navy Department Gazetteer, H. O. Pub. No. 881, July, 1944.

Locality	*Remarks*	*Lat. S.*	*Long. E.*
Arnavon Id.	(Isabel group, off northwest coast)	7°26′	158°01′
Ata (see Atta)			
Atta, Malaita Id.	(cove area on northeast coast)	8°31′	160°50′
Auki, Malaita Id.	(village on west coast)	8°47′	160°43′
Banika Id.	(2nd largest in Russell group)	9°05′	159°13′
Bio Id.	(San Cristobal group, off north coast)	10°10′	161°41′
Fauro (Faro) Id.	(Bougainville group, off south coast)	7°47′	158°37′
Florida Id.	(Nggela group, between Guadalcanal and Malaita Ids.)	9°05′	160°16′
Fulakora Pt., Isabel Id.	(east coast near southern end)	8°21′	159°51′
Gatukai Id.	(New Georgia group, southeast end)	8°47′	158°12′
Gela Id.	(not positively known, perhaps in Florida group)		
Gizo Id.	(New Georgia group, northwest end)	8°05′	156°49′
Ganongga Id.	(see Ronongo Id.)		
Kirigi River area, Florida Id.		9°08′	160°16′
Kolombangara Id.	(New Georgia group, northwest end)	8°00′	157°05′
Mono Id.	(Bougainville group, south end)	7°22′	155°35′
Munda, New Georgia	(southwest coastal area of New Georgia)	8°19′	157°15′

Locality	*Remarks*	*Lat. S.*	*Long. E.*
Narovo Id.	(New Georgia group, southwestern end)	8°16′	156°31′
Nggela Id.	(see Florida Id.)		
Puruata Id.	(Bougainville group, off western coast)	6°15′	155°05′
Rendova Id.	(New Georgia group, off southwestern coast)	8°31′	157°20′
Ronongo Id.	(New Georgia group, northwest end)	8°03′	156°35′
Roviana Lagoon area, New Georgia Id.		8°16′	157°17′
Rubiana Lagoon area	= Roviana Lagoon area		
Russell Id.	(between New Georgia and Guadalcanal)	9°04′	159°12′
Santa Ana Id.	(San Cristobal group, southeast end)	10°50′	162°28′
Santa Ysabel Id.	(see Isabel Id.)		
Simbo Id.	(see Narovo Id.)		
Shortland Id.	(Bougainville group, southern end)	7°03′	155°47′
Stirling Id.	(Bougainville group, southern end)	7°25′	155°35′
Tenaru River	(Guadalcanal Id., north coast)	9°25′	160°07′
Tertere area	(Guadalcanal Id., north coast)	9°25′	160°14′
Torokina Pt. area	(Bougainville Id., west coast)	6°22′	155°01′
Treasury Id.	(see Mono Id.)		
Tulagi Id.	(small island in Florida group)	9°06′	160°09′
Ugi Id.	(San Cristobal group off northeast coast)	10°14′	161°44′
Vangunu Id.	(New Georgia group off southeast end)	8°39′	158°00′
Vella Lavella Id.	(New Georgia group, northwest end)	7°43′	156°40′
Yandina, Pavuvu Id.	(Russell group)	9°07′	159°13′

List of Nomenclatural Changes

Platymantis weberi = *Platymantis papuensis weberi*
Rana bufoniformis = *Discodeles bufoniformis*
Rana guppyi = *Discodeles guppyi*
Rana opisthodon = *Discodeles opisthodon*
Rana krefftii = *Rana papua krefftii*

List of Amphibians Known From the Solomon Islands

BUFONIDAE Page
Bufo marinus marinus (Linné) 17
HYLIDAE
Hyla lutea Boulenger 19
Hyla thesaurensis Peters 20

RANIDAE

Page
Batrachylodes trossulus Brown and Myers 24
Batrachylodes vertebralis Boulenger 26
Ceratobatrachus guentheri Boulenger 29
Cornufer guppyi Boulenger 32
Cornufer neckeri Brown and Myers 34
Discodeles bufoniformis (Boulenger) 37
Discodeles guppyi (Boulenger) 39
Discodeles opisthodon (Boulenger) 42
Palmatorappia solomonis (Sternfeld) 44
Platymantis aculeodactylus sp. nov. 46
Platymantis myersi Brown 48
Platymantis papuensis weberi Schmidt 50
Platymantis solomonis (Boulenger) 53
Rana (*Hylarana*) *papua krefftii* Boulenger 56
Rana (*Hylarana*) *papua novaebritanniae* Werner 58

List of Extralimital Amphibians Discussed in the Text

Cornufer vitiensis (Girard), 1853 ..... 12, 32
Discodeles bufoniformis cognatus (Hediger), 1934 36
Discodeles ventricosus (Vogt), 1912 36
Platymantis beauforti (van Kampen), 1913 ..... 12, 48
Platymantis cheesmanae Parker, 1940 ..... 12, 46
Platymantis corrugatus (A. Duméril), 1853 50
Platymantis papuensis papuensis Meyer, 1874 50
Platymantis vitianus (A. Duméril), 1853 ..... 12, 48
Rana papua papua Lesson, 1830 12

Notes on the Geology and Geography of the Solomon Islands

A study of the relationship of any element of the fauna of these islands to corresponding elements in surrounding island areas necessitates some consideration of the general features of their geology and geography. This is necessary in order to determine the possible bearing of these factors on the distributional and evolutionary patterns which systematic considerations suggest.

Chubb (1934, pp. 289–302) calls attention to the fact that the andesitic zone which borders the Pacific shores of the American and Asiatic continents includes a roughly quadrangular, submerged area extending far into the Pacific Ocean from southeastern Asia. Its northeastern border extends from the island of Honshu through the Caroline Islands to a point just northeast of the Fijis; the shorter southeastern border extends southwestward to a point near the eastern shore of South Island, New Zealand; the long southwestern border lies between Australia and New Guinea and along the southern shores of the lesser Sundas, Java and Sumatra. This area is presumed to represent a continental extension subjected to extensive fracture and eruptive emergence during Mesozoic and Tertiary times. Many of the island groups within these limits tend to lie in northwest-southeast lines or arcs in the form of ridges but partly raised above the level of the ocean. These marginal, exposed ridges, according to one hypothesis, have probably never been directly connected to the adjacent continental mass. The fluctuations in the level of the now submerged portions of these ridges and the interlying basins can be presumed only on the indirect evidence of floral and faunal relationships and the direct evidence buried beneath the ocean floor (see also Myers, 1950).

The Solomons Archipelago forms a double chain some 600 miles in length (exclusive of the Santa Cruz group). This extends in a west-northwest to east-southeast line and apparently forms a continuation of the ridge system occupied by New Ireland and the Admiralty Islands. There are seven major groups of islands in the Solomons: the Bougainville, Choiseul, Isabel and Malaita groups on the north chain; the New Georgia, Guadalcanal and San Cristobal on the south. These do not represent two strictly parallel ridges, however. Bougainville, Choiseul, Isabel and Guadalcanal groups rest on one continuous undersea plateau which is submerged to a depth of not more than 600 fathoms; the other groups, New Georgia, Malaita and San Cristobal, are separated from this plateau and from each other by basins of greater depth, 1000 to 2000 fathoms (Lever, 1937, p. 272).

The larger islands, as Guadalcanal and Bougainville, are marked by a series of volcanic peaks, generally inactive in very recent history, which may attain heights of 8,000 to 10,000 feet.

Old volcanic rocks are now covered by sedimentary rocks generally only at lower altitudes, having been denuded at heights above 600 to 1000 feet. There is evidence, however, based on these remaining sedimentary rocks, that they were formed, in part at least, at depths of 12,000 feet or more beneath the surface of the ocean. This, if true, attests to the great orogenic changes which have taken place in this region.

The distances which now separate these major island groups within the Archipelago as well as that between the most northern group and the Bismarck Islands are not great. This in correlation with certain features of climate and ocean currents may have some bearing on the distribution of some elements of the fauna. These distances are given in the following table to the nearest mile (+ or −) as determined from the U. S. Navy hydrographic charts, 1945 edition (Nos. 5593, 5912, 2896, 2926, 5967, and 2920).

New Guinea	Rooke (Umboi)	29−
Rooke	New Britain	12±
New Guinea	Manus (Admiralties)	175
Manus	Mussau	150
New Britain	New Ireland	20+
New Ireland	Nissan Island	70−
Nissan	Buka	42−
New Ireland	Buka	105
Buka	Bougainville	2 or 3
Bougainville	Shortland	6+
Bougainville	Fauro	9−
Shortland	Mono	17+
Mono	Vella Lavella	60+
Bougainville	Choiseul	30+
Vella Lavella	Kolombangara	15−
Kolombangara	Arundel	1±
Arundel	New Georgia	2−
Choiseul	Rob Roy	1±
Rob Roy	Wagina	5+
Wagina	Arnavon	12±
Arnavon	Gagi	12−
Wagina	Gagi	26+
Gagi	Barola	1±
Barola	Isabel	1±
Isabel	New Georgia	65+
Isabel	Malaita	50−
Isabel	Florida	35−
Isabel	Guadalcanal	50−
Florida	Guadalcanal	15−
New Georgia	Vangunu	1±
Vangunu	Gatukai	5−
Gatukai	Pavuvu	60+
Gatukai	Guadalcanal	100
Pavuvu	Guadalcanal	32+
Florida	Malaita	25+
Guadalcanal	Malaita	32+
Guadalcanal	San Cristobal	35±
Guadalcanal	Rennell	105
San Cristobal	Rennell	100
San Cristobal	Malaita	40−

The breadth of the present ocean basins between the larger islands of the seven primary groups ranges from about 25 to 100 miles. It should be noted, however, that the greater distances are in all instances reduced by the presence of small islands at intermediate points. These small islands might well function as stepping stones in the process of faunal dispersal by flotsam methods.

The humid, tropical climate and heavy rainfall support a rich covering of vegetation, mainly tropical forest. There are, however, extensive grassy areas on some of the larger islands, Guadalcanal, for example (Guppy, 1887b, p. 25). Short, often large, and generally rapid streams occur on the islands but freshwater lakes are few.

Nature and Distribution of the Amphibian Fauna

The amphibian fauna of the Solomon Islands is zoogeographically very interesting because of the highly endemic nature of its ranid component and the fact that this Archipelago is, with the Fijis and New Zealand, a Pacific amphibian outpost. Three genera, *Batrachylodes, Ceratobatrachus* and *Palmatorappia,* are known only from the Solomons. *Discodeles* has been recorded for the Bismarcks and the Admiralties outside of the Solomons. *Cornufer* and *Platymantis* have more extended ranges. Both are represented by distinct species in the Fiji Islands to the east (see Brown and Myers, 1949a), while *Platymantis* ranges west to Borneo and *Cornufer* as far as Burma. Both occur also in the Philippines.

All of these genera (*Batrachylodes* possibly excepted) are apparently closely related, as held by Noble (1931, pp. 522–524). They are possibly descended from a single, more primitive ranid stock. However, further work both from the anatomical and embryological approaches is needed in order to outline with greater assurance the probable lines of evolution within the group and to reconstruct the theoretical prototype or prototypes.

The close relationship between *Ceratobatrachus, Cornufer, Discodeles* and *Platymantis* is shown not only in such skeletal features as the broadly forked omosternal style and the large, broad nasals, but also in certain reproductive modifications. The eggs of species within these genera, as far as I have been able to observe (fourteen of twenty-nine recognized species), are relatively large and unpigmented. This suggests that the larvae of all the species may complete their development within the egg capsule as is, indeed, known for *Cornufer guentheri* and *Discodeles opisthodon.* Maturing, ovarian eggs of *Palmatorappia* are unpigmented.

In *Batrachylodes* the omosternal style is unforked and it may possibly be derived from a hylaranid stock as Noble (1931, p. 521) proposes for *Micrixalus* and *Simomantis*. However, eggs of *B. trossulus* are relatively large and unpigmented and a modification of developmental habits similar to that of the genera *Cornufer* and *Discodeles* is also suggested for this genus.

The Solomons representatives of *Platymantis* and *Cornufer*, the only two genera having ranges known to extend much beyond the Archipelago, appear to have their closest affinities with Fijian and New Guinean species. In the first-mentioned genus *P. solomonis* is probably most closely related to *P. vitianus* of the Fijis, both are very large, rather smooth forms; *P. aculeodactylus* is closely related to *P. cheesmanae* of New Guinea; *P. myersi* may have its closest affinities with *P. beauforti* of New Guinea; and *P. papuensis weberi* is regarded as but subspecifically differentiated from *P. papuensis papuensis* of New Guinea. In the second genus *C. guppyi* is related to *C. vitiensis* of the Fijis but is a larger form, while *C. neckeri* is a very distinct species and appears not to be related closely to other known forms.

The presumably phylogenetically older hylids, so numerous in Australia and New Guinea, are represented by only two known species. One of these, *Hyla thesaurensis*, is also recorded from New Guinea.[1] *Rana* (*Hylarana*) is also known from only two representatives and both are regarded as subspecifically related to the common New Guinean form, *Rana* (*Hylarana*) *papua papua*. The members of these two genera, as far as known from the Solomons, lay small, typically pigmented eggs. This suggests, as is known for *Hyla thesaurensis*, that the eggs are laid in permanent or semi-permanent bodies of water and that the larvae undergo a period of development and metamorphosis after hatching.

Thus the amphibian fauna of the Solomons appears to be comprised of two elements. The older element is a rather closely related, possibly diphyletic, endemic group of highly specialized ranid frogs, the members of *Batrachylodes*, *Ceratobatrachus*, *Cornufer*, *Discodeles*, *Palmatorappia*, and *Platymantis* (in part). The more recent element appears to include members of *Hyla*, *Rana* (*Hylarana*) and two (possibly three) species of *Platymantis*.

The older ranid element has its present center of abundance in the Solomons Archipelago and possibly the Bismarcks. Only two of the genera, as already noted, have ranges much beyond this region. Two hypothetical explanations are suggested for the more extended ranges of *Platymantis* and *Cornufer:* (1) that they represent the older, more widely dispersed, possibly ancestral genera as held by Noble (1931, pp. 521–524) or (2) that they have simply been the more successful in spreading through an island range.

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[1] The possible subspecific status of this New Guinean population remains for future investigation.

The specialization of large, unpigmented eggs, and probably general practice of direct development, parallels that of certain plethodontids, brevicipitids, and leptodactylids. Such a specialization, it may be hypothesized, could have enabled these frogs to maintain themselves near their present center in the Solomon Islands at some time in the past, under conditions when permanent or semipermanent bodies of still or slow moving water may have been less readily available as breeding sites. On the other hand, the Hylas and Hylaranas, which on the basis of their closer affinities with the New Guinean forms would appear to be later arrivals, may have been able only to invade or at least maintain themselves in the Solomons when suitable breeding sites became more generally available. To this group of later arrivals would also belong the two (or three) species of *Platymantis*, which are very closely related to the Papuan species.

Geological evidence, as far as known, would in general be consistent with this hypothesis of a possible change in the physical nature of the islands in relatively recent times. There has been a general uplifting of many of the islands to a height of sometimes hundreds of feet (Guppy, 1887b, pp. 125–136). Their general profile suggests that prior to this they may have been even more steep and rugged, mountainous islands with more limited marginal lowland areas.

When the amphibian faunas of different island groups within the Solomons are compared, in contrast to comparisons of the fauna of the Archipelago as a whole with those of the Bismarcks and New Guinea, a striking general homogeneity is observed. This is modified in two ways, however: (1) the northern group of islands, Bougainville and Choiseul, appear to have a richer amphibian fauna and San Cristobal at the extreme south the poorest; (2) inter-island subspecific populations are known for some species and when more extensive collections become available may be substantiated for others.

The more limited fauna of the San Cristobal group suggests that the southern part of the chain has perhaps always been more completely isolated and lends support to the hypothesis that the island groups (or perhaps the four primary, submarine plateaus) have always been more or less separated by barriers such as marine basins which have acted as distributional filters. At the same time, the two factors, (1) a homogeneous, highly endemic fauna and (2) a fauna apparently derived from at least two invasions widely separated in time, suggest a probably greater isolation of the Archipelago as a whole at some intermediate period in the past and also possibly closer connections between at least some of the island groups within the Archipelago.

DISTRIBUTIONAL CHART OF AMPHI

		Bougainville Group								Isabel Group		New Geo Grou	
	Solomon Islands	Buka	Bougainville	Puruata	Fauro (Faro)	Shortland (Alu)	Mono (Treasury)	Stirling	Choiseul	Arnavon	Isabel (Santa-Ysabel)	Vella Lavella	Ronongo (Ganongga)
Bufo m. marinus													
Hyla lutea			○ –				T ○		–				
Hyla thesaurensis	–	○	* + ○ –	–	–	*	T * ○ –				* –		
Batrachylodes trossulus			T –						–				
Batrachylodes vertebralis		+	–		T * ○						○		* –
Ceratobatrachus guentheri	–		○ –		T * ○ –	T * ○ –	T * ○ –	–	–		* ○ –	–	
Cornufer guppyi			○ –		* ○		T * ○ –		* –	–	* ○ –		*
Cornufer neckeri			T –										
Discodeles bufoniformis			○ –		* ○		T * ○ –		–		○ –	–	–
Discodeles guppyi			○ –		* ○	T * ○					* ○		
Discodeles opisthodon	–		–		T ○ –	○	T ○						
Palmatorappia solomonis		T ○ –									+		
Platymantis aculeodactylus			T –						–				
Platymantis myersi			T –										
Platymantis papuensis weberi			–								* ○ –	–	
Platymantis solomonis		○	○ –	–	T * ○	T * ○	T * ○ –	–	–	–	○ –		
Rana papua krefftii													
Rana papua novaebritanniae			–								*1 + –		

T Type locality.
– Specimens identified in present study.
○ Reported in the literature but not examined in the present study.
+ Based on records in the literature of species regarded as synonyms.
* Reported to be in the collections of the British Museum (Natural History).
1 Specimens in the British Museum which are here referred to *novaebritanniae* are catalogued as *krefftii*. However, on the basis of the present study these islands are occupied by the subspecies *novaebritanniae*.

IE SOLOMONS ISLANDS

New Georgia Group				Russell Group			Guadalcanal Group					San Cristobal Group					
New Georgia	Rendova (Hammond)	Vangunu	Gatukai	Russell Islands	Pavuvu	Banika	Guadalcanal	Savo	Florida (Nggela)	Tulagi	Malaita	San Cristobal	Ugi	Bio	Malaulalo	Malaupaino	Santa Ana
						○ –	○ –										
–				* –	–		+ * –		+	–	–						
–						–	–			○	○ –		○				–
* –	–	–		* –		–	* ○ –	*	○ –	○ –	○ –						
							○ –				–						
*										–	–		○				
*	–		–				* ○ –		–		–						
												–	–				–
*		–					* –			T ○ –	–						
–		–								–	○ –						
												T * ○ –		–		*	* –
							+ *1 –			–	+ –						

I. A specimen from Fauro Island in the British Museum, referred by Boulenger (1887) to *Cornufer dorsalis*, is regarded as an error and is not recorded here.

II. Specimens of *Hyla thesaurensis* and *Ceratobatrachus guentheri* in the British Museum from Gela Island are not shown in the chart. The exact location of this island is unknown to me, but it is suspected that it may be a small island perhaps in the Florida group.

III. Two specimens, reported as *Cornufer corrugatus* by Sternfeld (1920 [1921]) from Buka Island, may be either *Platymantis papuensis weberi*, *P. solomonis* or possibly some other species and hence are not shown on the chart.

The probability of occasional population interchanges between islands by rafting is supported by the observations of Guppy (1887b, pp. 125–144). Commenting on the rapid denudation of the higher parts of the islands, he describes the frequent torrential flooding of the streams and the extensive muddying of the sea by this debris for a distance of at least a third of a mile from shore following the frequent heavy tropical rains. He also comments on the extensiveness of the pumice drift reaching the shores of the Solomons following the volcanic eruption at Blanche Bay, New Britain, May 1878, borne there by the eastward-moving ocean currents.

Further geological information concerning past land fluctuations in this general region of the Pacific basin area may in the future help to clarify our understanding of some rather puzzling distributions and may point the way to a better understanding of phylogenetic relationships.

Treatment of Data in the Systematic Section

The descriptions of the species which are discussed in the systematic part are sufficiently detailed, it is hoped, to enable workers to avoid some of the errors in identification to which overly brief descriptions have frequently lent themselves in the past. Whenever sufficiently large series of mature or near-mature specimens were available from any one island, such series were the only ones used in determining the means and their standard errors of measurements or body proportions given in the descriptions. This was done to facilitate comparisons by those working with series from other islands where possible island races may exist.

Measurements were made as follows: length of head, along the side from the tip of the snout to the posterior edge of the tympanum unless otherwise stated; breadth of head, at the angle of the jaws; diameter of the eye, along the anteroposterior axis; length of tibia, in the flesh.

Body proportions used were: (1) head width/length from snout to vent, head width/length of tibia, length of tibia/length from snout to vent, diameter of eye/head width, diameter of tympanum/head width, and diameter of tympanum/diameter of eye. The mean and its standard error are given in each case.

When samples of populations were compared to determine the possible significance of differences in the means of measurements or body proportions, Student's "t" was calculated taking into consideration the small size of the samples.

For the sake of brevity the following abbreviations have been used throughout the text with reference to collections of various institutions:

American Museum of Natural History (A.M.N.H.), California Academy of Sciences (C.A.S.), Museum of Comparative Zoölogy, Harvard (M.C.Z.), Museum of Vertebrate Zoology, University of California (M.V.Z.), San Diego Society of Natural History (S.D.S. N.H.), Natural History Museum, Stanford University (S.N.H.M.), United States National Museum (U.S.N.M.).

SYSTEMATIC DISCUSSION

Key to the families of amphibians in the Solomon Islands

1. The halves of the pectoral girdle fused ventrally........Ranidae
   The halves of the pectoral girdle overlapping ventrally.........2
2. Intercalary cartilages present; terminal phalanges claw-shaped...Hylidae
   Intercalary cartilages absent; terminal phalanges straight or nearly so (not claw-shaped)..................................Bufonidae

BUFONIDAE

The only representative of this family known from the Solomon Islands, *Bufo marinus marinus* (Linné), was introduced, presumably early in 1940 (Lever, 1945, p. 1).

Genus BUFO Laurenti

BUFO MARINUS MARINUS[1] (Linné)

Rana marina Linné, 1758, Systemae Naturae (ed. 10), p. 211: America.
Bufo marinus Lever, 1945, p. 1.

26 larvae (M.C.Z. 26008–9) Guadalcanal Id. (L. W. Jarcho) 1944.
2 (U.S.N.M. 119624–5) Lunga area, Guadalcanal Id. (D. H. Johnson) 1944.
6 larvae (A.M.N.H. 51958) Guadalcanal Id.
12 (M.V.Z. 39648–59) Banika Id. (J. A. Gray) 1944.
2 (M.V.Z. 40731–32) Guadalcanal Id. (Lowell Adams) 1944.
1 (S.D.S.N.H. 18019) Guadalcanal Id.

Description. Head broader than long; snout rounded; canthus rostralis forming a prominent crest continuous with the preorbital and supraciliary crests; postorbital crest reaching a point almost as far ventral as the center of the tympanum; supratympanic crest extending from the postorbital portion of the supraciliary crest to the anterior border of the parotid gland; loreal region nearly vertical, tuberculate; interorbital region concave with scattered, moderate warts; parotid glands large, heavily pitted, reaching posterior to the axillary region; upper eyelids strongly rugose; roof of mouth with a transverse ridge just posterior to the choanae, strongly projecting laterally but low near the mid-point; tongue broadly oval without a median notch posteriorly.

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[1] These specimens have been compared with the description of *Bufo marinus paracnemis* (Lutz).

Forelimb well developed; first finger much longer than the second; subarticular tubercles moderately large, rounded, less broad than the subtending digit; inner metacarpal tubercle narrow; outer broadly oval; hindlimb relatively short, heels failing to meet when limbs are folded at right angles to the body; length of the tibia somewhat less than, or equal to, the breadth of the head; toes about 1/3 webbed, the distal 3 phalanges of the fourth toe being free; subarticular tubercles small, round to oval, narrower than the subtending digit; inner metatarsal tubercle prominent, narrowly oval or elliptical; outer smaller, less protrudent; dorsum and lateral surfaces marked by rows of warts, those of the dorsum larger; venter granulate, granules with brown-tipped centers except in the region of the hindlimbs; limbs profusely tuberculate or warty on upper surfaces.

Color of the Marine Toad, as in its native habitat, the tropical New World, is highly variable. The dorsum (in preservative) shows various shades of brown or gray. The top of the head, middorsal line and lateral surfaces are generally lighter as are the larger warts and tubercles. The warts and tubercles are, however, brown-tipped. The venter is grayish or yellowish, somewhat marbled with darker gray or brown.

It may be noted that tadpoles were collected on Guadalcanal both in June and November.

Range. Definitely known from Guadalcanal, Malaita and Banika as well as perhaps other islands in the Russell group. This species has also been introduced into the Admiralties; U.S.N.M. 121854–5 are from Manus Island and 121660–2 are from Los Negros.

HYLIDAE

Genus HYLA Laurenti

Parker (1939, p. 2) regarded *H. lutea* as definitely distinct from *H. thesaurensis* whereas van Kampen (1923, p. 50) was somewhat doubtful following Barbour's relegating it to the synonymy of the latter (Barbour 1921, p. 93). Parker noted among other characters the more extensive webbing of the fingers, the larger size and the longer, more pointed snout of *H. lutea*. That the snout is longer is not borne out by the present series, its ratio to head width or total length being approximately the same for both species. However, the distinctness of *H. lutea* from *H. thesaurensis* in other respects is amply evidenced.

The following key serves to separate these two species:

Head moderately depressed; disk of third finger generally smaller than tympanum; disks of fingers (except the inner one) much broader than the subtending digit which is not bordered by a wide flange of skin. . . .*thesaurensis*

Head much depressed; disk of third finger generally larger than tympanum; disks of fingers not or scarcely broader than the subtending digit which is bordered by a wide flange of skin. . . . .*lutea*

HYLA LUTEA Boulenger

(Pl. 4, fig. 2)

Hyla lutea Boulenger, 1887, Proc. Zool. Soc. London, 1887, p. 337, pl. xxviii, fig. 4; Fauro Id., Solomon Ids. (Type in British Museum).

Hyla thesaurensis (part), Burt and Burt, 1932, p. 488.

Cornufer guppyi (part), Burt and Burt, 1932, p. 489.

4 (A.M.N.H. 34273, 35342, 35344–5) Bougainville Id. (Whitney Exped.).
3 (A.M.N.H. 34636–7, 35387) Choiseul Id. (Whitney Exped.).
1 (S.N.H.M. 9346) Bougainville Id. (Exch. Amer. Mus.).

Description. Head slightly less broad to as broad as long, its breadth about 1/3 the length from snout to vent; snout round-pointed; eye moderate, its diameter about 1/3 the breadth of the head; tympanum round, its diameter 1/2 or slightly more than that of the eye; loreal region strongly oblique, concave; canthus rostralis rounded, rather indistinct; interorbital space broader than upper eyelid; vomerine teeth in two transverse patches between the choanae and almost in contact medially; tongue broadly oval and but feebly indented at the mid-point of the posterior margin.

Forelimb well developed; finger tips strongly depressed with large disks; disks broader than long (except for the inner finger), but scarcely broader than the subtending digits as measured to include the flanges of skin on the lateral margins; fingers more extensively webbed than in *H. thesaurensis*, the third finger being webbed to the subdistal tubercle on the outside and to a point between this and the basal tubercle on the inside, the second almost to the distal tubercle on the outside; subarticular tubercles small, low, transversely elongate; metacarpal tubercles indistinct; hindlimb long, length of tibia about 3/5 the length from snout to vent; disks of toes smaller than those of fingers; subarticular tubercles small, more strongly protrudent than those of hands; inner metatarsal tubercle narrow elliptical, its length less than its distance from the basal tubercle of the inner toe; outer absent; toes webbed almost to the disks except for the fourth; skin smooth except for the flat granules of the lower surfaces of the thighs and abdomen.

Color (in preservative) of the dorsum is quite uniformly grayish or yellowish tan for these eight specimens; somewhat lighter on the venter.

Measurements	♂(S.N.H.M. 9346)	♀(A.M.N.H. 34273)
Snout to vent..............	54 mm.	65.5 mm.
Snout length................	9 “	11 “
Head length (to base of skull)	16 “	19 “
Head breadth..............	17 “	22 “
Eye diameter..............	6 “	6.5 “
Tympanum diameter.......	3 “	3.75 “
Tibia length................	30 “	39 “

Range. Known from Bougainville, Mono and Choiseul Islands.

HYLA THESAURENSIS Peters

(Pl. 3, figs. 1, 2)

Hyla thesaurensis Peters, 1877, Monatsb. Akad. Wiss. Berlin, p. 421: Treasury Id., Solomon Ids. (Type in Berlin).

Hyla macrops Boulenger, 1883, Ann. Mag. Nat. Hist. (5), xii, p. 164: Treasury Id., Solomon Ids. (Type in British Museum).

Hyla solomonis Vogt, 1912, Sitzb. Ges. Naturf. Freunde Berlin, p. 10: Bougainville Id., Solomon Ids. (Type probably in Berlin).

Hyla thesaurensis (part), Burt and Burt, 1932, p. 488.

1	(M.C.Z. 7373) Fulakora, Isabel Id.	(W. M. Mann)	1916.
2	(“ 7374–75) Auki, Malaita Id.	“	“
3	(“ 7376–8) Tulagi Id.	“	“
10	(“ 7379–88) Atta, Malaita Id.	“	“
3	(“ 7390, 7392–93) Isabel Id.	“	“
4	(“ 7401–4) Yandina, Pavuvu Id.	“	“
1	(“ 7405) Rubiana Lagoon area, New Georgia Id.	“	“
1	(“ 9374) German Solomon Ids.	(Exch. Berlin Mus.)	1922.
1	(“ 26051) Guadalcanal Id.	(L. W. Jarcho)	1943.
2	(“ 26052–3) “ “	“	1943.

1 (S.N.H.M. 8390) Tetere area, Guadalcanal Id. (J. P. Heath) 1944.
2 (C.A.S. 49952–3) Guadalcanal Id. (J. A. Kusche) 1920.
6 (" 49956–61) " " " 1921.
1 (" 54665) Malaita Id. (W. M. Mann) 1916.
1 (" 72100) " " (Crocker Exped.) 1933.
24 (U.S.N.M. 119560–5, 119567–75, 119756–64) Torokina Pt., Bougainville Id. (W. L. Necker and D. H. Johnson).
38 juvs. and larvae (U.S.N.M. 119765) Torokina Pt., Bougainville Id. (W. L. Necker and D. H. Johnson).
1 (U.S.N.M. 119566) Puruata Id. (W.L. Necker and D.H. Johnson).
1 (" 119721) Mono Id. " "
2 (M.V.Z. 40733–4) Malumba River area, Guadalcanal Id. (Lowell Adams) 1944.
3 (M.V.Z. 44189–90, 44223) lower Lunga River area, Guadalcanal Id. (J. Chattin) 1944.
2 (S.D.S.N.H. 18057–8) Russell Ids.
4 (A.M.N.H. 34320, 35327, 35339, 35346) Bougainville Id. (Whitney Exped.) 1930.
1 (A.M.N.H. 35423) Mono Id. (Whitney Exped.) 1930.
1 (" 39998) Central Malaita Id. (Whitney Exped.) 1930.
72 ♂♂, ♀♀, juvs., and larvae (A.M.N.H. 51959–75) Guadalcanal Id. 1944.
8 ♂♂, ♀♀ (A.M.N.H. 52173, 52176–79) Guadalcanal Id. 1945.

Hyla thesaurensis is highly variable as to color and may prove to be constituted of at least two geographical races or be undergoing such differentiation. Only from the southwestern islands have I observed occasional specimens heavily mottled with dark-brown on the throat and chin. However, the majority of the specimens from these islands possesses the uniformly light venter and lower lip. Therefore I have chosen to regard *H. thesaurensis* as a highly variable species until larger series are available from many more of the islands.

Description. Head slightly less broad to as broad as long, its breadth about 1/3 the length from snout to vent, depressed but less so than for *H. lutea;* snout rounded, its length less than 1/2 the breadth of the head (45.99% ± .692 for 24 specimens from the Bougainville group); eye moderate, its diameter 1/3 to about 2/5 the breadth of the head (38.18% ± .647 for 24 specimens); tympanum large, its diameter generally about 1/2 that of the eye (49.83% ± 1.44 for 24 specimens); interorbital space broader than the upper eyelid; loreal region slightly oblique, shallowly concave; canthus rostralis distinct, slightly rounded; vomerine teeth in two short, narrowly separated, transverse or slightly oblique patches between the choanae or their posterior borders; tongue broad with a shallow notch at the mid-point of the posterior margin.

Forelimb well developed; fingers with large, rounded or transversely elliptical disks at the tips; disks (except for inner finger) much broader than the subtending digit which is bordered at most by only a narrow flange of skin on the lateral margins; disk of third finger much smaller than, or equal to, the tympanum; fingers with slight or moderate webs, reaching the basal tubercle on the inside and about halfway between the basal and subdistal tubercles on the outside of the third finger, and the subdistal tubercle on the outside of the second; subarticular tubercles moderately protrudent (except the distal ones), transversely elliptical; inner metacarpal tubercle narrow elliptical; middle and outer shorter; hindlimb long, tibia length about 1/2 to 3/5 the length from snout to vent (58.42% ± .514 for 24 specimens); disks of toes somewhat smaller than those of fingers; subarticular tubercles moderate, round or transversely elongate, smaller than those of hands; inner metatarsal tubercle narrow elliptical, short, its length less than its distance from the subarticular tubercle of the inner toe; outer small, round; toes webbed almost to the disks except for the fourth; skin smooth on the dorsum or occasionally with a few, scattered granulations; venter with moderate granules posterior to the pectoral region and sometimes on the chin as well; lower proximal region of the thighs granular.

Color (in preservative) of the dorsum highly variable, being light-grayish to olive-brown, often with darker mottling; the three white lines along the back, as originally described by Peters (1877, p. 421) and figured by Boulenger (1886, fig. 4), present or absent, or broken, more commonly present in juveniles but also in some adults; venter white, yellowish or tan, throat and chin sometimes mottled with brown as observed for specimens from Guadalcanal Island.

Mature ovarian eggs are small and pigmented at the animal pole region.

Measurements	♂(U.S.N.M. 119569)	♀(U.S.N.M. 119721)
Snout to vent	40.5 mm.	49 mm.
Snout length	6 "	7 "
Head length (to posterior edge of tympanum)	13.5 "	17 "
Head breadth	12.5 "	17 "
Eye diameter	5 "	6.25 "
Tympanum diameter	2.5 "	3 "
Tibia length	23 "	28.5 "

Range. (see distributional chart)

Since a description of the larval stage of this species has apparently not been recorded in the literature the following notes are given, based on a series of larvae and transforming individuals (U.S.N.M. 119765).

One of the younger larvae with the forelimbs rather well developed but still beneath the operculum, measures 58 mm. in total length; vent to tip of tail 38 mm.; width of body 12 mm. (preserved condition); nostril to tip of snout 3 mm.; eye to nostril 3 mm.; interorbital space 6 mm.; width of mouth 4 mm.; greatest breadth of tail 9 mm. The mouth is antero-ventral in position. The lips are papillate except for the median third of the upper lip; the upper lip possesses two rows of horny teeth, the inner divided at the midline. The lower lip has three rows, the inner one also medianly divided. The edges of the jaws have a dark horny covering. The eyes are dorsolateral in position. The spiracle forms a narrow slit-like opening (1 mm. in length) slightly ventral to a line connecting the corner of the mouth and the groin on the left side and about equidistant from these two points of reference. The dorsal and ventral fins of the tail are of approximately equal width with the tip rounded, and heavily pigmented (dark grayish-brown in preservative).

RANIDAE

The following key will serve to distinguish the genera of the Ranidae known to occur in the Solomon Islands:

1. Omosternal style entire or with a very small notch at the base.........2
   Omosternal style with a broad fork at the base......................3
2. Vomerine teeth present; toes with webs................*Rana* (*Hylarana*)
   Vomerine teeth absent; toes without webs.................*Batrachylodes*
3. Vomerine teeth absent; fingers with webs................*Palmatorappia*
   Vomerine teeth present; fingers without webs.........................4
4. Terminal phalanges broadly T-shaped; digital disks large; toes moderately webbed..*Cornufer*
   Terminal phalanges bluntly rounded...............................5
5. Digital disks small to large; toes moderately to almost fully webbed *Discodeles*
   Digital disks small; toes without webs..............................6
6. Odontoids absent from lower jaw.......................*Platymantis*
   Odontoids present on lower jaw......................*Ceratobatrachus*

Genus BATRACHYLODES Boulenger

This genus was originally set up by Boulenger (1887, p. 337) on the basis of a single female specimen of *B. vertebralis* from Fauro Island. Neither at that time nor in his later writings did he mention the possible relationship of *Batrachylodes* to other ranid genera. Noble (1931, p. 524), apparently without having seen a specimen, held it to be a diminutive relative of *Cornufer* lacking vomerine teeth. Deckert (1938, p. 181), who also was unable to examine a specimen of the genus, follows Noble.

This proposed derivation from *Cornufer*, however, is not borne out when one examines closely the pectoral girdle. The omosternum, though broad at the base, is unforked. On the basis of this evidence, although *Batrachylodes* may have been derived from the same ranid stock as *Platymantis* and *Cornufer*, the undivided omosternum makes possible its origin in the *Hylarana* group as Noble (1931, p. 521) proposes for *Micrixalus* and *Staurois*.

Eggs are large and unpigmented as observed for *Batrachylodes trossulus*.

The following key serves to distinguish the two known species:

Disks of fingers and toes little dilated; breadth of disk of third finger about half diameter of tympanum	*trossulus*
Disks of fingers and toes broadly dilated; breadth of disk of third finger equal to or greater than diameter of tympanum	*vertebralis*

BATRACHYLODES TROSSULUS Brown and Myers

(Pl. 6, fig. 3; Pl. 8, fig. 1)

Rana solomonis (part), Burt and Burt, 1932, p. 491.

Batrachylodes trossulus Brown and Myers, 1949b, Jour. Wash. Acad. Sci., vol. 39, no. 11, pp. 379–80; Torokina, Bougainville Id. (Type in United States National Museum).

7 (U.S.N.M. 119577 holotype, 119586–88, 119787–89) Torokina Pt., Bougainville Id. (W. L. Necker).

1 (A.M.N.H. 35425) Choiseul Id. (Whitney Exped.).

As no additional specimens of this small frog have been found in collections examined since its description was published in 1949, nothing more is known of its variability, and only a brief restatement of that description is given here.

Description. Head relatively narrow, its breadth about 1/3 the length of the body, 2/3 to 3/5 the length of the tibia; snout rather pointed, strongly projecting beyond the tip of the lower jaw, its length about 1/3 to 1/2 the breadth of the head; eye large, its diameter about equal to or slightly greater than the length of the snout; diameter of tympanum slightly more or less than 1/2 the diameter of the eye; loreal region nearly vertical; canthus rostralis somewhat rounded; vomerine teeth absent; tongue oval without a distinct notch posteriorly.

Forelimb moderately developed; fingers slender with small round disks at their tips, much smaller than in *B. vertebralis;* the inferior portion of the disk separated from the superior by a nearly terminal crescentic groove; diameter of the disk of the third finger about 1/2 that of the tympanum; terminal phalanx a narrow "T"; subarticular tubercles poorly or moderately developed; inner metacarpal tubercle broadly oval, moderate; middle one similar in size and development; outer one smaller; hindlimb rather well developed; length of the tibia about half the length of the body; heel reaching the eye; tips of toes expanded into large disks, larger than those of the fingers and slightly broader than long; subarticular tubercles moderately developed; inner metatarsal tubercle oval, elongate, its length about equal to its distance from the end of the outer toe; outer metatarsal tubercle moderate, round; toes without webs; skin smooth.

Color (in preservative) very uniform for the entire series from Bougainville Island; dorsum dusky gray suffused with pale reddish, most prominent on the hindlimbs; sides of head and body dark reddish-brown to black, bordered above by a light edge and continuous with the dark blotch on anteroventral surface of the forelimb; axillary surface of forelimb with an uneven-edged, dark slate or blackish band; as is also the anterior border of the thigh; anterior surface of lower leg with a more or less broken series of dark blotches or dashes; anal region and proximal portion of posterior surface of thighs blackish; under surface of head, throat and pectoral region dark reddish-brown with scattered light flecks; white nuptial tubercles on the chin and sometimes throat of males, belly and under surface of thighs whitish flecked with dark reddish-brown.

Ovarian eggs are unpigmented, large.

Measurements	♂(U.S.N.M. 119577)	♀(U.S.N.M. 119586)
Snout to vent............	20.25 mm.	19 mm.
Snout length.............	3 "	2.5 "
Head length (to posterior edge of tympanum).....	7 "	6.25 "
Head breadth............	6.5 "	6.5 "
Eye diameter.............	3 "	3 "
Tympanum diameter......	1.5 "	1.25 "
Tibia length..............	10 "	9.25 "

Range. Known from Bougainville and Choiseul Islands.[1]

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[1] The Choiseul specimen differs greatly in color pattern from the Bougainville series and may represent a distinct race (see Brown and Myers 1949b).

BATRACHYLODES VERTEBRALIS Boulenger

(Pl. 1, fig. 1; Pl. 2, fig. 2; Pl. 6, fig. 2)

Batrachylodes vertebralis Boulenger, 1887, Proc. Zool. Soc. London, 1887, p. 337, pl. xxviii, fig. 3: Fauro Id., Solomon Ids. (Type in British Museum).

Chaperina fredericii Sternfeld, 1920 (1921), p. 435. (Type in Senckenberg Museum).

Sphenophryne wolfi Sternfeld, 1920 (1921), p. 435. (Type in Senckenberg Museum).

Platymantis solomonis (part), Barbour, 1921, p. 96.

Cornufer guppyi (part), Barbour, 1921, p. 97.

Cornufer guppyi (part), Burt and Burt, 1932, p. 489.

3 (M.C.Z. 7449–51) Rubiana Lagoon area, New Georgia Id. (W. M. Mann) 1916.
1 (M.C.Z. 7452) Santa Ana Id. (W. M. Mann) 1916.
4 (M.C.Z. 7455, 7457, 7589–90) Atta, Malaita Id. (W. M. Mann) 1916.
1 (A.M.N.H. 35427) Ronongo Id. (Whitney Exped.).
1 (M.V.Z. 44191) lower Lunga River, Guadalcanal Id. (J. Chattin) Aug. 8, 1944.
1 (M.V.Z. 44977) Munda, New Georgia Id. (C. G. Sibley) Nov. 4, 1944.
16 (U.S.N.M. 119576, 119578–79, 119581–85, 119589, 119782–86, 119790–91) Torokina Pt., Bougainville Id. (W. L. Necker).

A re-examination of collections reported by Barbour (1921) and Burt and Burt (1932) shows the difficulty of distinguishing the young of this small frog from the young of other Solomons ranids. Barbour (1921, p. 95) originally listed three specimens from New Georgia Island in the W. M. Mann collections. Five other specimens were erroneously identified as the young of *Cornufer guppyi* (M.C.Z. 7452 from Santa Ana Island, 7455 and 7457 from Malaita Island) and as the young of *Platymantis solomonis* (M.C.Z. 7489–90 from Malaita Island). Burt and Burt (1932, p. 489) similarly referred a small male (A.M.N.H. 35427 from Ronongo Island) to *Cornufer guppyi*. Mertens (1929, p. 266) has shown that specimens used by Sternfeld (1920 [1921], p. 435) as the basis for describing *Chaperina fredericii* and *Sphenophryne wolfi* actually were specimens of *Batrachylodes vertebralis* (see also Brown and Myers, 1949b, p. 379).

Description. Breadth of head slightly greater than its length or about equal to it; snout round-pointed, its length somewhat less than half the breadth of the head (43.79% ± 1.187 for 13 specimens from Bougainville), projecting beyond the lower jaw (the thickened, whitish tip mentioned by Barbour [1921, p. 95] appears in varying degree in both males and females); white nuptial tubercles present on the ventral surface of the head region of males, varying greatly in frequency from a few near the tip of the lower jaw to a scattering over the entire under surface of the head and throat; nostril about equidistant from the tip of snout and eye; eye large, its diameter about 1/3 to 2/5 the breadth of the head (38.88% ± .596 for 13 specimens); loreal region nearly vertical, flat; canthus rostralis distinct, rounded; interorbital distance much greater than the breadth of the upper eyelid; tympanum covered by a thin skin, the diameter about 1/2 that of the eye (47.69% ± 2.091 for 13 specimens); vomerine teeth absent; tongue narrow-oval, posterior margin entire and free.

Forelimb well developed; fingers stout with large disks, which are broader than long and generally somewhat truncate; breadth of disk of third finger generally greater than diameter of tympanum, dorsal and ventral portions of the expanded disk are separated by a wholly inferior, crescentic groove, not continued across the lower surface at the proximal edge of the disk; inner metacarpal tubercle large, oval, moderately projecting; middle one low and broadly oval; two outer ones small and low; subarticular tubercles rather large, rounded; fingers without webs; hindlimb moderately developed, length of tibia about equal to, or 2/5 greater than, the breadth of the head, less than half the length from snout to vent (47.3% ± .876 for 13 specimens); tibiotarsal articulation reaching the tympanum or the eye; tips of toes with disks, but smaller than those of fingers, inferior and superior parts of disks separated in a manner similar to that of fingers; inner metatarsal tubercle rather strongly projecting, elliptical; outer low, rounded, smaller; subarticular tubercles, moderately large, rounded; skin of dorsum and lateral surfaces smooth or with a few short folds, particularly on the upper lateral surfaces; posterior surface of thighs usually with large, flat granules.

Color (in preservative) is highly variable and for that reason somewhat detailed color notes of three specimens, all from Torokina Point, Bougainville Island, follow:

U.S.N.M. 119578 almost uniformly grayish on the dorsum, upper lateral surfaces and limbs; a black bar extending on either side from near the tip of the snout across the loreal region to the eye and thence posteriorly to the region of the shoulder; ventral surfaces and margins of the lips whitish, the latter, as well as the limbs, head and throat regions, speckled with grayish-brown.

U.S.N.M. 119581 grayish on the dorsum and limbs, the latter with distinct, darker, transverse bars becoming narrower on the fingers and toes; irregular black flecks and spots on the dorsum and lateral surfaces; a white dorsolateral band from the posterior part of the upper eyelid to the groin; loreal regions, sides of head and margins of the jaws grayish-brown, the latter indistinctly marked with narrow, white transverse bars; ventral surfaces white, heavily flecked with grayish-brown except on the abdomen.

U.S.N.M. 119786 grayish on the anterior part of the head; grayish-rose or red on the back, lateral surfaces and limbs, the latter with dark transverse bands; dorsum and lateral surfaces also heavily marked with black including an irregular transverse bar between the eyes and two somewhat indistinct anteriorly pointed chevrons on the back; sides of the head, loreal areas and mid-lateral regions are blackish, margins of lips lighter, the lower with rather distinct, narrow, white, transverse bars; ventral surfaces heavily flecked with brown.

Occasional specimens (as M.C.Z. 7455 and 7457) exhibit the light vertebral stripe emphasized by Boulenger in describing the type.

Measurements	♂ (U.S.N.M. 119578)	♀ (U.S.N.M. 119782)
Snout to vent	28.25 mm.	23 mm.
Snout length	5 "	3.25 "
Head length (to posterior edge of tympanum)	10 "	8 "
Head breadth	10.5 "	8 "
Eye diameter	4 "	3 "
Tympanum diameter	2 "	1.5 "
Tibia length	11.5 "	10.5 "

Range. (see distributional chart)

Genus CERATOBATRACHUS Boulenger

Boulenger (1884, p. 212) in describing this genus placed it in a distinct family on the basis of the toothed condition of the lower jaw and the undilated sacral diapophyses. Later (1910, pp. 149–156) he suppressed the family, noting that the tooth-like, bony projections of the lower jaw were less significant than once supposed in the Salientia. Noble (1931, p. 523) points out the close affinities of this genus with *Platymantis* from which it differs primarily in possessing odontoids and in the more extensive bony deposits in the squamosal and ethmoid regions of the skull. Only a single species is known. Boulenger (1886, pls. xii-xiii) gives fine illustrations of the variability in color pattern and the striking appearance of this frog.

The pupil is horizontal; vomerine teeth are present; omosternal style is forked at the base. Outer metatarsals are united, fingers and toes are without webs or nearly so. The terminal phalanges are bluntly rounded.

Ovarian eggs are large and unpigmented.

CERATOBATRACHUS GUENTHERI Boulenger

(Pl. 2, fig. 5; Pl. 5, fig. 2)

Ceratobatrachus guentheri Boulenger, 1884, P.Z.S. London, 1884, p. 212: Treasury, Shortland and Fauro Ids. (Type in British Museum).

2 (M.C.Z. 2207; 2 cotypes) Fauro Id. (Exch. Brit. Mus.).
12 (" 7464, 7466–75, 7588) Malaita Id. (W. M. Mann) 1916.
3 (" 7476–78) Tulagi Id. (W. M. Mann) 1916.
4 (" 7479–82) Isabel Id. " 1916.
1 (" 26084) Stirling Id. (L. W. Jarcho) 1945.
2 (A.M.N.H. 5334–35) Malaita Id. (W. M. Mann) 1916.
1 (" 22858) Vangunu Id. (Whitney Exped.) 1928.
2 (" 22859–60) Rendova Id. " " 1928.
104 (" 34275–307, 35235–95, 35297–301, 35336–37) Bougainville Id. (Whitney Exped.).
1 (A.M.N.H. 35373) Shortland Id. (Whitney Exped.).
2 (" 35374, 35440) Mono Id. " "
4 (" 35381, 35399, 35431–32) Guadalcanal Id. (Whitney Exped.).
9 (A.M.N.H. 35384, 35400, 35413–18, 35422) Kolombangara Id. (Whitney Exped.).
4 (A.M.N.H. 34638, 35388, 35552, 35554) Choiseul Id. (Whitney Exped.).
5 (A.M.N.H. 35393–94, 35408–10) Russell Ids. (Whitney Exped.)
1 (" 35395) Narovo Id. " "
4 (" 35397–98, 35411–12) Florida Id. " "
6 (" 35402–03, 35419–20, 35428–30, 35433) Ronogo Id. (Whitney Exped.).
1 (A.M.N.H. 35426) Gizo Id. (Whitney Exped.).
2 (" 35434–35) Vella Lavella Id. " "
5 (" 36437–41) Auki, Malaita Id. " "
10 (" 39986–96) central Malaita Id. (Whitney Exped.) 1930.
3 (A.M.N.H. 51745; 2 uncat.) near Cape Hunter, Guadalcanal Id. (Whitney Exped.) 7/20/1927.
2 (A.M.N.H. 51952–53) Guadalcanal Id. 1945.
1 (U.S.N.M. 20066) Solomon Ids. (Edward Girard).
1 (" 61163) Malaita Id. (W. M. Mann) 1916.
2 (" 118254–55) Atta, Malaita Id. " 1916.
14 (" 119552–58, 119749–55) Torokina Pt., Bougainville Id. (W. L. Necker and D. H. Johnson).
3 (M.V.Z. 44193, 44224–25) lower Lunga River, Guadalcanal Id. (John Chattin) 7/11/1944.
1 (M.V.Z. 44947) Munda, New Georgia Id. (Chas. G. Sibley) 11/4/1944.
64 (C.A.S. 72101–64) Malaita Id. (Crocker Exped.).

2 (S.N.H.M. 8391–92) Torokina Pt., Bougainville Id. (J. P. Heath) 1943.
1 (S.N.H.M. 9337) Bougainville (Exch. American Museum Natural History) 1948.
1 (S.N.H.M. 9338) Malaita (Exch. American Museum Natural History) 1948.

Description. Head triangular in shape, broader than long (in young specimens about as broad as long), much depressed; breadth about ½ the length from snout to vent (52.28% ± .707 for 12 specimens from Bougainville); snout long, pointed; eye moderate, its diameter about 1/5 to 1/4 the breadth of the head (23.11% ± .574 for 12 specimens); tympanum large, oval, its vertical diameter much greater than its horizontal diameter, somewhat less than, or equal to, that of the eye; nostril much nearer the tip of snout than the eye; loreal region strongly oblique, slightly concave; canthus rostralis angular; vomerine teeth in two short, slightly oblique or transverse, widely separated patches behind the choanae or between their posterior edges; tongue oval with a broad or moderately narrow, shallow notch at the mid-point of the posterior free margin.

Forelimb well developed; fingers long, slender; tips bluntly rounded, or slightly swollen; subarticular tubercles large, generally as broad as the subtending digit, round to oval, generally more protrudent distally; inner metacarpal tubercle short, broadly oval, strongly protrudent; middle one more narrow, low, outer small and low; hindlimb moderate; length of tibia about 4/5 the breadth of the head (81.72% ± 1.08 for 12 specimens); tips depressed, moderately dilated into somewhat pointed disks, the inferior pad separated from the superior portion by a terminal, crescentic groove (except that the inner and outer toes, particularly the latter, may often show this groove indistinctly or not at all); subarticular tubercles smaller than those of fingers, round to oval, strongly protrudent, pointed distally; inner metatarsal tubercle moderate in length, elliptical, strongly protrudent; outer small and round; toes without webs; skin occasionally rather smooth with prominent, protrudent, triangular, dermal flaps only on the upper eyelids and tip of the snout, and narrow, irregular, dorsal folds scarcely evident; but generally with prominent dermal flaps also along the limbs and at the angles of the jaws and with narrow, elongate, irregular folds along the body above the dorsolateral region and along the lower limbs, and with a few short, transverse folds on the dorsum as well as the prominent ones across the interorbital and internasal spaces.

Color (in preservative) of the dorsum highly variable, light gray or tan, almost uniform or with some scattered darker spots; grayish suffused with reddish or dusky; reddish-brown; or almost black. Thighs usually with narrow, transverse, dark bands; venter whitish, spotted with brown on head and throat, or heavily suffused with light-brown or sometimes blackish-brown.

Ovarian eggs are large and unpigmented. A juvenile (M.C.Z. 7588) measures only 10 mm. from snout to vent.

Measurements	♂ (U.S.N.M. 119553)	♀ (U.S.N.M. 119554)
Snout to vent	65 mm.	80 mm.
Snout length	13 "	15 "
Head length (to posterior edge of tympanum)	25 "	35 "
Head breadth	30 "	40 "
Eye diameter	8 "	9 "
Tympanum diameter	7 "	7 "
Tibia length	27 "	33 "

Range. (see distributional chart)

Genus CORNUFER Tschudi

Platymantis was re-separated from *Cornufer* by Boulenger (1918b, p. 372) and in keeping with this treatment of these two groups the latter may be defined as ranid frogs with broadly dilated finger tips, the disks of which are usually larger than those of the toes. There is generally a transverse proximal groove on the ventral surface (indistinct or lacking in some of the small Philippine species and perhaps in others) which is continuous laterally with the crescentic groove between the inferior and superior portions of the disk; the toes are moderately webbed or webbed only at the base; the terminal phalanx is a broad "T" with the horizontal expansion straight or somewhat curved. The omosternal style is broadly forked at the base. Fully developed ovarian and uterine eggs are large and unpigmented where known.

The two species known to occupy the Solomon Islands may be distinguished as follows:

Head narrow, its breadth generally less than 2/5 the length from snout to vent; loreal region slightly or moderately oblique; snout strongly protrudent, rather pointed; groove surrounding ventral pad of finger and toe disks wholly inferior	*neckeri*
Head broad, its breadth generally more than 2/5 the length from snout to vent; loreal region strongly oblique; snout not or little protrudent, round or round-pointed; groove surrounding ventral pad of finger and toe disks distally terminal or superior	*guppyi*

Cornufer guppyi Boulenger

(Pl. 2, fig. 3; Pl. 5, fig. 4)

Cornufer guppyi Boulenger, 1884, Proc. Zool. Soc. London, 1884, p. 211: Treasury Id. (Type in British Museum).
Cornufer dorsalis, Boulenger, 1887, p. 337.
Cornufer guppyi (part), Barbour, 1921, p. 97.
Cornufer guppyi (part), Burt and Burt, 1932, p. 489.

1 (M.C.Z. 7453) Isabel Id. (W. M. Mann) 1916.
1 (" 7456) Atta, Malaita Id. " "
4 (" 7458–59, 7461–62) Auki, Malaita Id. " "
12 (A.M.N.H. 34267, 34271, 34308, 34310, 35313, 35318–19, 35338, 35349–52) Bougainville Id. (Whitney Exped.).
1 (A.M.N.H. 34635) Choiseul Id. (Whitney Exped.).
1 (" 35370, 35390, 35424) Mono Id. " "
1 (" 35380) Guadalcanal Id. " "
1 (" 35385) Arnavon Id. " "
2 (" 39999–40000) Malaita Id. " "
1 (S.N.H.M. 9339) Bougainville Id. (Exch. Amer. Mus.) 1948.
1 (C.A.S. 54721) Auki, Malaita Id. (Exch. Mus. Comp. Zool.) 1921.
1 (" 72165) Malaita Id. (Crocker Exped.) 1933.

In his original description Boulenger did not state what he believed to be the relationship of this species to other members of the genus. Later, however, (1886, p. 54) he related it to *C. dorsalis* (= *vitiensis*) from the Fiji Islands, distinguished on the basis of its relatively broader, depressed head and the larger disks of the fingers and toes. The close affinities of these two species are evident but the fact that they may also be distinguished on the basis of structural characters of the finger disks has been shown by Brown and Myers (1949a, pp. 4–7). *C. guppyi* is also a much larger species, for female specimens up to 60 mm. from snout to vent do not show evidence of maturity whereas a 45 mm. specimen of *C. vitiensis* from Viti Levu Island is gravid.

Description. Head broad and much depressed, more prominently so in older and larger specimens, its breadth greater than its length and generally more than 2/5 the length from snout to vent (43.10% ± 1.234 for 5 specimens from Malaita Island); snout rounded, scarcely protrudent beyond the lower jaw, its length 1 1/3 to 1 2/3 the diameter of the eye; eye moderate, its diameter 1/5 to 3/10 the breadth of the head (27.38% ± 1.574 for 5 specimens); tympanum round, its diameter about 1/2 that of the eye and about 1/6 the breadth of the head (14.94% ± 1.118 for 5 specimens); canthus rostralis rounded; loreal region strongly oblique, concave; nostril nearer tip of snout than eye; vomerine teeth in two small to moderate, transverse or somewhat oblique patches, between or behind the posterior edges of the choanae, generally separated by more than the length of one of them; tongue broadly obovate with a rather deep notch at the mid-point of the posterior free margin.

Forelimb well developed, first finger shorter than the second; tips of fingers dilated into large disks, broader than long, the inferior pad separated from the superior portion of the disk by a dorsally subterminal, crescentic groove which is continuous laterally with the transverse groove across the ventral surface proximally; a prominent, distally-pointing, groove on the dorsal surface near the middle of the expanded portion; subarticular tubercles large, round or somewhat truncate proximally, generally as broad as the subtending digit, only slightly or moderately protrudent, inner metacarpal tubercle large, broadly elliptical or oval, its length equal to its distance from the distal end of the large tubercle of the first finger, middle one narrower, outer small, oval or elliptical or may be indistinct; hindlimb well developed, length of tibia slightly more or less than 1/2 the length from snout to vent (50.37% ± .604 for 5 specimens); tips of toes with large disks, slightly smaller than those of fingers, broader than long and with ventral pad completely surrounded by a groove as on the fingers; subarticular tubercles moderate to large, round to oval, often somewhat truncate distally, moderately protrudent; inner metatarsal tubercle moderately wide, elliptical, its length greater than its distance from the distal end of the tubercle of the first toe; outer small or moderate, round to oval, sometimes poorly defined; metatarsal area somewhat granulate; toes with moderate webs, reaching distally to the subarticular tubercle on the outside of the second toe, and to the subarticular tubercle on the outside of the third toe, dorsum almost smooth, upper lateral surfaces finely granulate or tuberculate; venter posterior to the pectoral region with moderate flat granules; posterior surface of thighs more finely granulate.

Color (in preservative) of dorsum and upper lateral surfaces highly variable, light tan almost white, grayish or dark reddish-brown, variously blotched or marbled with darker brown to blackish-brown, occasionally with a narrow white middorsal line; margin of lips more or less the same color as the dorsum; hindlimbs and frequently the forelimbs also with narrow to moderate dark transverse bars; venter whitish or light tan often blotched or speckled with brown anterior to the pectoral region.

Ovarian eggs large and unpigmented.

Measurements	♂(M.C.Z. 7456)	♀(M.C.Z. 7462)
Snout to vent	33 mm.	98 mm.
Snout length	6 "	16 "
Head length (to posterior edge of tympanum)	13 "	35 "
Head breadth	15 "	47 "
Eye diameter	4.5 "	10.5 "
Tympanum diameter	2 "	5 "
Tibia length	17 "	47 "

Range. (see distributional chart)

CORNUFER NECKERI Brown and Myers

Cornufer guppyi (part), Burt and Burt, 1932, p. 489.
Cornufer neckeri Brown and Myers, 1949a, Amer. Mus. Nov., no. 1418: Bougainville Id. (Type in American Museum of Natural History).
21 (A.M.N.H. 34268, 34270, 34309, 34311–19, 34322–23, 34329 holotype, 34525, 35331–35) Bougainville Id. (Whitney Exped.).
1 (S.N.H.M. 9335) Bougainville Id. (Exch. Amer. Mus.) 1948.

The *Rhacophorus*-like appearance of this frog, particularly in relation to the digital expansions, is striking. However, the intercalary cartilage is not present and this is the principal character upon which the rhacophorid and ranid frogs are separated.

Since this species was described (Brown and Myers, 1949a) no additional specimens have been found in collections examined and only a brief restatement of the original description can be given at this time.

Description. Head about as broad as long, its breadth generally less than 2/5 the length from snout to vent (38.88% ± .388 for 6 specimens from Bougainville); snout rather pointed, generally projecting well beyond the lower jaw, its length about 1 1/4 to 1 1/3 times the diameter of the eye; eye large, its diameter about 1/3 to 2/5 the breadth of the head (36.95% ± 1.785 for 6 specimens); canthus rostralis rather sharp; loreal region slightly oblique, concave; tympanum round, its diameter generally less than 1/2 that of the eye and about 1/6 the breadth of the head (16.52% ± .64 for 6 specimens); vomerine teeth in two oblique, well separated patches behind the level of the choanae; tongue oval with a broad, shallow notch in the free posterior border.

Forelimb well developed; tips of fingers broadly dilated (except for the inner one); the inferior pad transversely elliptical, completely surrounded by a groove which distally is inferiorly subterminal; breadth of disk of third finger generally greater than the diameter of the tympanum; subarticular tubercles (except for the basal ones which are small, round and low) large, round to oval, strongly protrudent distally; inner metacarpal tubercle prominent, nearly twice as long as broad; middle one broadly oval, large; outer small, narrow, elliptical; hindlimb moderately long, length of tibia about 1/2 the length of the body (49.64% ± .747 for 6 specimens); tips of toes broadly expanded, but dilations smaller than those of fingers, ventral pads of disks transversely elliptical and completely surrounded by a groove similar to that of the fingers; toes webbed to the basal tubercle or slightly beyond; subarticular tubercles moderate, round to oval, most strongly projecting distally; inner metatarsal tubercle prominent, elliptical, 2 to 3 times as long as broad; outer distinct, smaller, round to oval; skin of the dorsum generally smooth or with a few small tubercles posteriorly; venter finely granulate posterior to the pectoral region as is also the proximal posterior surface of the thighs.

Color (in preservative) of the dorsum varies from grayish to dark-reddish, more or less uniform or with lighter and darker blotches. The upper surface of the thighs have more or less broad, narrowly separated, diagonally transverse bands. The venter is light grayish to tan, profusely flecked and spotted, especially anteriorly and on limbs.

Measurements	♂ (S.N.H.M. 9336)	♀ (A.M.N.H. 34325)
Snout to vent	48 mm.	56 mm.
Snout length	8.5 "	9 "
Head length (to posterior edge of tympanum)	17 "	20 "
Head breadth	18 "	22 "
Eye diameter	6.5 "	7 "
Tympanum diameter	3 "	4 "
Tibia length	24 "	27 "

Range. Known from Bougainville Island.

Genus DISCODELES Boulenger

Boulenger (1918a, p. 238) set up *Discodeles* as a subgenus of *Rana* to include *guppyi* (the type), *opisthodon* and *bufoniformis*, and revived, as a subgenus, *Hylarana* Tschudi to include *Rana kreffti* and four New Guinea species. In 1920 he gave a much more detailed account of the differences between these two groups. *Discodeles* was stated to have the omosternum forked at the base, outer metatarsals separated by a web only in the distal third, nasal bones large, in contact with each other and with the frontoparietals. It should also be noted that the terminal phalanx is bluntly rounded; the fingers free; and the toes moderately to almost fully webbed. To *Discodeles*, Boulenger also assigned six Indian and Malayan species and to *Hylarana* he added fifty-eight south Asiatic and one African species. He regarded *Discodeles* as leading to *Platymantis* and *Cornufer*.

Noble (1931, pp. 520–523) raised *Discodeles* to generic rank and regarded it as closely related to *Platymantis*. He also limited *Discodeles* in known range to the Solomon and Fiji Islands.[1] Although he did not state his reasons at this point he implied that all species of *Discodeles* probably practice direct development and this would of course eliminate the Asiatic frogs referred to this subgenus by Boulenger. Since this is probably a sound basis for limiting the natural group comprising *Discodeles*, following Noble I regard it as a genus distinct from *Rana*.

Three species of the genus are here recognized from the Solomons. Barbour's placing of *D. opisthodon* in the synonymy of *D. bufoniformis* (1921, p. 98) was an error as suspected by Schmidt (1932, p. 181). Van Kampen (1923, p. 186) actually retained *D. opisthodon* as a distinct species though expressing some doubt. The shorter legs and more toad-like form of adults, especially females, of *D. bufoniformis* as compared to *D. opisthodon* can be readily shown in the ratios: (1) width of head/length of tibia, (2) length of tibia/length from snout to vent. The tips of the toes are generally less expanded, more oval and pointed, for *D. bufoniformis*; the tips of the fingers less depressed and less dilated. Although the males and juveniles of *D. bufoniformis* cannot be readily distinguished from those of *D. opisthodon* on the basis of the above mentioned ratios, they generally can be rather easily separated on the basis of the pointed or simply swollen finger tips which lack entirely a terminal crescentic groove between the inferior and superior portions which is usually present for males and juveniles of *D. opisthodon*.

Discodeles bufoniformis is referred to in the binomial, for Hediger's (1934, p. 484) description of *D. bufoniformis cognatus* from Movehafen, New Britain, was, I believe, in error as to the closest affinities. *D. bufoniformis cognatus* was said to differ from *D. bufoniformis* in the smoother skin and the more strongly developed inner metatarsal tubercle, and from *D. ventricosus* (Vogt, 1912, p. 8) from the Admiralties on the basis of the greater length of the first finger, the greater length of the hindlimb and the more fully webbed toes. Although Hediger does not give measurements of the breadth of the head and the length of the tibia for his type and unique specimen, Vogt's measurements for *D. ventricosus* correspond to those of *D. opisthodon.* This suggests that *D. bufoniformis cognatus* is probably related to *D. opisthodon* or *D. guppyi* and should be re-examined in this light.

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[1] Noble's reference to the Fijis may have been a lapsus for Admiralty Islands since no member of *Discodeles* has ever been recorded for the Fijis as far as I can determine. Vogt (1912, p. 8) described *Discodeles ventricosus* from the Admiralty Islands.

The following key serves to distinguish the species of *Discodeles* known from the Solomon Islands.

1. Tips of fingers rather broadly dilated and depressed forming prominent disks; lower metatarsal surface smooth; vomerine tooth patches extending outward beyond the sagittal plane of the inner edge of the choanae; males with external vocal sacs; tibia very long, 1¼to 1½ times the breadth of the head at the angle of the jaws............................*guppyi*

   Tips of fingers not, or but moderately, dilated and depressed; lower metatarsal surface with numerous tubercles; vomerine tooth patches not extending outward beyond the sagittal plane of the inner edge of the choanae; males with internal vocal sacs............................2
2. Disks of toes generally oval, moderately pointed, only occasionally round; tips of fingers pointed or bluntly swollen (not dilated or depressed); length of tibia less than, or equal to, breadth of head (about 4/5 to 9/10 for adult females)....................................*bufoniformis*

   Disks of toes rather broad, round; tips of fingers generally somewhat dilated and depressed, a more or less distinct terminal, crescentic groove separating the dorsal and ventral portions; length of tibia about equal to breadth of head (slightly greater for adult females).........*opisthodon*

DISCODELES BUFONIFORMIS (Boulenger)

(Pl. 1, fig. 2; Pl. 2, fig. 4; Pl. 7, fig. 3)

Rana bufoniformis Boulenger, 1884, Proc. Zool. Soc. London, 1884, p. 210 Treasury Id. (Type in British Museum).
Rana (*Discodeles*) *bufoniformis*, Boulenger, 1918a, pp. 237–40.
Rana bufoniformis (part), Barbour, 1921, pp. 98–99.
Discodeles bufoniformis, Noble, 1931, p. 523.
Rana bufoniformis (part), Burt and Burt, 1932, pp. 489–90.
Rana kreffti (part), Burt and Burt, 1932, p. 490.

1 (M.C.Z. 7413) Auki, Malaita Id. (W. M. Mann) 1916.
4 (" 7414–17) Isabel Id. " "
2 (" 7428–29) Tulagi Id. " "
7 (A.M.N.H. 35375, 35377–79, 35392, 35441–42) Mono Id. (Whitney Exped.).
6 (A.M.N.H. 35443–48) Choiseul Id. (Whitney Exped.).
21 (" 35450–70) Ronongo Id. " "
2 (" 35437–38) Vella Lavella Id. " "
1 (S.N.H.M. 9342) Ronongo Id. (Exch. Amer. Mus.) 1916.
1 (" 9343) Choiseul Id.
22 (U.S.N.M. 119595–610, 119766–71) Torokina Pt., Bougainville Id. (W. L. Necker and D. H. Johnson).

Boulenger (1920, p. 110) had still seen only two adult specimens of *D. bufoniformis*, the type from Treasury (Mono) Island and one from Fauro Island, when he reviewed the Ranas of the western Pacific regions.

Island (geographical) races of this species are indicated in some characters but it seems unwise to attempt to delimit races until such time as more specimens are available from many of the islands. I have seen a series of more than six adult specimens from only two islands, Bougainville and Ronongo.

Description. Head broad, depressed, its breadth for mature specimens about 2/5 to 1/2 the length from snout to vent (46.32% ± 1.35 for 22 specimens from Ronongo); snout broadly rounded (pointed only in young individuals); eye large, its diameter about equal to the length of the snout, 1/4 to almost 1/3 the breadth of the head (25.5% ± .311 for 22 specimens); tympanum round, its diameter 2/5 to 1/2 that of the eye (43.45% ± .597 for 22 specimens); interorbital space as broad or broader than the upper eyelid; loreal region strongly oblique, concave; canthus rostralis rounded; vomerine teeth in two oblique patches, generally separated by a distance equal to the length of one of them, posterior to the choanae and not extending out on either side to the sagittal plane of the inner border of the choanae; tongue broadly oval with a moderate to broad notch at the mid-point of the free posterior margin; vocal sacs internal.

Forelimb well developed; tips of fingers pointed in young, bluntly rounded or more often swollen in adults, not depressed; first finger longer than second; subarticular tubercles large, rounded or slightly pointed distally; inner metacarpal tubercle large, broadly elliptical or oval; middle and outer ones more or less distinct, somewhat shorter than the inner one and generally merging proximally; fingers without webs; hindlimb moderately developed, length of tibia much less than breadth of head for adult females (88.72% ± .482 for 22 specimens), slightly less than, or equal to, breadth of head for males and juveniles; tips of toes depressed, with slightly or moderately expanded disks, generally somewhat pointed, the inferior pad being separated from the superior part by a crescentic, distally subterminal groove; subarticular tubercles moderately large, oval, more pointed distally; lower surface of the metatarsal region with numerous small tubercles; inner metatarsal tubercle elongate, elliptical, prominent; outer small, round; webs generally reaching the disks of the first and fifth toes, the distal tubercle on the outer side and the penultimate tubercle on the inner side of the fourth; skin of the dorsum and limbs strongly rugose with numerous small to large porous warts, more or less in elongate folds on the upper lateral surfaces; upper surface of the head (except the eyelids) rather smooth; venter and lower surface of the thighs generally granulate.

Color (in preservative) of the dorsum grayish-brown, to light-brown or dark reddish-brown; ventral surfaces whitish or yellowish, more or less powdered with grayish-brown or light-brown.

Uterine eggs are large and unpigmented, measuring 7 mm. in diameter (65% alcohol preservation) as observed in U.S.N.M. 119770 from Bougainville.

Measurements	♂(U.S.N.M. 119595)	♀(U.S.N.M. 119770)
Snout to vent	78.5 mm.	134 mm.
Snout length	11.5 "	22 "
Head length (to posterior edge of tympanum)	24 "	46 "
Head breadth	34 "	58 "
Eye diameter	11 "	17.5 "
Tympanum diameter	4.25 "	6.5 "
Tibia length	32 "	49 "

Range. (See distributional chart).

Variation. The entire series (U.S.N.M. 119595–610, 119766–71) from Torokina Point, Bougainville Island, exhibit a smoother dorsum and a generally lighter coloration of the venter than the series (A.M.N.H. 35450–70) from Ronongo Island in the New Georgia group. However, on comparison of the two topotypes, A.M.N.H. 35442 is found to be much more warty than A.M.N.H. 35441. The series of specimens (A.M.N.H. 35443–48) from Choiseul possess somewhat more broadly expanded disks at the tips of the toes, but otherwise show no differences. Parker (1939, p. 2) has called attention to the much larger size of the adult females as compared to the adult males. The probability (P) that the dimorphism, exhibited by the present series of four mature females and three mature males from Bougainville Island, is a result of chance sampling is extremely low as shown by the "t" value for the difference between the means. In the following table n = degrees of freedom.

	Male	Female	diff.	t	n	P
Mean of	($N_1 = 3$)	($N_2 = 4$)				
snout to	76.17 mm.	129 mm.	52.83	13.21	5	∠.001
vent length	±1.30	±3.24				

Discodeles guppyi (Boulenger)

Rana guppyi Boulenger, 1884, Proc. Zool. Soc. London, 1884, p. 211: Shortland Island. (Type in British Museum).

Rana (*Discodeles*) *guppyi* Boulenger, 1918a, pp. 239–40.
Discodeles spp., Noble, 1931, p. 523.
Rana bufoniformis (part), Burt and Burt, 1932, pp. 489–90.
Rana guppyi (part), Burt and Burt, 1932, p. 490.
Rana krefftii (part), Burt and Burt, 1932, p. 490.

1 (M.C.Z. 3503) Guadalcanal Id. (Exch. Brit. Mus.) 1914.
3 (" 7548–50) Malaita Id. (W. M. Mann) 1916.
1 (" 22309) Guadalcanal Id. (Exch. Brit. Mus.) 1916.
1 (" 26054) Guadalcanal Id. (L. W. Jarcho) 1944.
2 (A.M.N.H. 22853–54) Rendova Id. (Whitney Exped.)
1 (" 22855) Gatukai Id. " "
3 (" 34326, 34330–31) Bougainville Id. " "
1 (C.A.S. 49964) Guadalcanal Id. (J. A. Kuche) 1921.
19 (" 72081–99) Malaita Id. (Crocker Exped.) 1933.
1 (U.S.N.M. 63400) Malaita Id. (W. M. Mann) 1916.
2 (" 119772–73) Torokina, Bougainville Id. (W. L. Necker)
1 (S.N.H.M. 9344) Bougainville Id. (Exch. Amer. Mus.) 1948.

Rana guppyi was described by Boulenger (1884, p. 211) on the basis of a single female specimen from Shortland Island. Later (1920, p. 214) he recorded specimens from islands as far south as Isabel and Guadalcanal. At this time he gave a more complete description and called attention to certain characters, as the relatively much greater length of the hindlimbs, which some later workers have failed to use.

Thus Burt and Burt (1932, p. 490) erroneously placed specimens from Gatukai and Rendova Islands, which belong to this species, under *R. bufoniformis*, basing their assignment on the wartiness of the skin of the dorsum and granulation of the venter and thighs. These three specimens from Rendova and Gatukai are darker reddish-brown ventrally, more granulate on thighs and venter, and with more numerous fine warts on the dorsum than are the other specimens examined. Should such differences remain constant for specimens from the New Georgia group of islands, they might well constitute a valid race of *D. guppyi*, but they are, regardless of the warty nature of the skin, wholly unlike *D. bufoniformis* or *D. opisthodon*.

Description. A very large frog, reaching a length from snout to vent of at least 195 mm. (M.C.Z. 26054); head broader than long, its breadth about 2/5 the length from snout to vent (39.34% ± .278 for 19 specimens from Malaita); snout rounded to somewhat pointed, little or moderately protrudent beyond the lower jaw, long, its length somewhat less than or equal to 1/2 the breadth of the head; nostril about twice as far from the eye as the tip of the snout; eye moderate, its diameter 1/4 or somewhat greater than 1/4 the breadth of the head (27.32% ± .36 for 19 specimens); tympanum round, its diameter about 1/3 to nearly 1/2 that of the eye (41.09% ± .929 for 19 specimens); loreal region moderately oblique; canthus rostralis distinct; vomerine teeth in two transverse or slightly oblique patches, behind or with their bases between the choanae, their crests straight or curved and extending laterally beyond the sagittal plane of the inner borders of the choanae, the patches separated by a distance not more than twice the length of either series; tongue oval in shape, free posteriorly, with a moderate to deep, rather narrow notch at the mid-point of the posterior margin; vocal sacs external.

Forelimb well developed; fingers with strongly depressed, expanded disks at the tips, the inferior pad separated from the superior portion by a deep, crescentic, terminal or dorsally subterminal groove; subarticular tubercles large, round or broadly oval, inner metacarpal tubercle large, broadly elliptical, its length equal to its distance from the distal end of the subarticular tubercle of the inner finger; the middle and outer smaller and broadly oval; hindlimb long, length of the tibia 1¼ to 1½ times the breadth of the head; tips of toes with broad, strongly depressed disks, the inferior pad separated from the superior portion by a crescentic groove as on the fingers; subarticular tubercles moderate in size, oval and more strongly protrudent distally; metatarsal region smooth; inner metatarsal tubercle narrow-elongate; outer small and round; dorsum generally rather smooth except along the dorsolateral regions, or with small to moderate tubercles over the entire dorsal surfaces (as in A.M.N.H. 22855); posterior venter and posterior surface of the thighs of many specimens covered with moderate, flat granules, or nearly smooth.

Color of the dorsum (in preservative) varies from light reddish-brown to dark reddish-brown or blackish-brown, more or less uniform or with darker blotches. The limbs may be somewhat lighter. The venter is usually yellowish or whitish with grayish-brown or brownish suffusion of the chin and throat; or more uniformly reddish-brown (as in A.M.N.H. 22855). The margins of the lips may be uniformly light or may show broad, dark transverse bars (as in S.N.H.M. 9344).

Ovarian eggs are large and unpigmented.

Measurements	♂ (A.M.N.H. 22855)	♀ (C.A.S. 72094)
Snout to vent	128 mm.	170 mm.
Snout length	23 "	29 "
Head length (to posterior edge of tympanum)	42.5 "	51 "
Head breadth	51 "	64 "
Eye diameter	14 "	16 "
Tympanum diameter	5 "	7 "
Tibia length	64 "	86 "

Range. (See distributional chart).

DISCODELES OPISTHODON (Boulenger)

(Pl. 7, figs. 1, 2)

Rana opisthodon Boulenger, 1884, Proc. Zool. Soc. London, 1884, p. 211: Treasury and Fauro Ids. (Types in British Museum).
Rana bufoniformis (part), Barbour, 1921, p. 98.
Discodeles opisthodon, Noble, 1931, pp. 64, 523.
Rana bufoniformis (part), Burt and Burt, 1932, pp. 489–90.
Rana guppyi (part), Burt and Burt, 1932, p. 490.
Rana bufoniformis Slevin, 1934, p. 184.
Rana opisthodon, Boulenger, 1918a, p. 238.
1 (M.C.Z. 3591) Solomon Ids. (Exch. Australian Mus.) 1914.
6 (" 7408,[1] 7423–27) San Cristobal Id. (W. M. Mann) 1916.
4 (" 7409–12) Ugi Id. (may be San Cristobal). (W. M. Mann) 1916.
1 (M.C.Z. 7431) Santa Ana Id. (W. M. Mann) 1916.
1 (" 22310) Solomon Ids. (Exch. Brit. Mus.).
1 (A.M.N.H. 35436) Fauro Id. (Whitney Exped.).
7 (" 34274, 34327–28, 35354, 35356–58) Bougainville Id. (Whitney Exped.).
1 (A.M.N.H. 35421) Kolombangara Id. (Whitney Exped.).
1 (U.S.N.M. 63401) Ugi Id. (W. M. Mann) 1916.
1 (C.A.S. 72247) Ugi Id. (Crocker Exped.) 1933.
1 (S.N.H.M. 9345) Bougainville Id. (Exch. Amer. Mus.) 1948.

Description. Head broader than long; its breadth usually less than 1/2 the length from snout to vent (43.92% ± .58 for 5 specimens from Bougainville and Fauro Islands); snout generally somewhat pointed; nostril nearer tip of snout than eye; eye moderate, its diameter about 3/5 to 4/5 the length of the snout, 1/4 to occasionally 1/3 the breadth of the head (30.62% ± 1.103 for 8 specimens); tympanum round, its diameter about 1/3 to 1/2 that of the eye (39.06% ± 1.308 for 8 specimens); loreal region oblique, moderately concave; canthus rostralis distinct, somewhat angular; vomerine teeth in two oblique patches behind the choanae or with the anterior portion of their bases between the choanae, not extending out beyond the sagittal plane of the inner edges of the choanae, patches separated by a distance generally equal to or greater than the length of either of them; tongue broadly oval, free posteriorly, with a narrow to broad, rounded notch at the mid-point of the posterior margin; vocal sacs internal.

Forelimb well developed; tips of fingers depressed, moderately dilated, the inferior pad separated from the superior part by a more or less distinct, crescentic, terminal groove, especially in males and juveniles; subarticular tubercles large, round to somewhat oval; palmar area finely tuberculate; inner metacarpal tubercle broadly elliptical, outer one about equal to it in length but narrower, middle one shorter broadly oval; fingers without webs; hindlimb well developed, the length of the tibia about equal to the breadth of the head (98.62% ± 1.676 for 8 specimens, 101.95% ± 3.69 for 3 large females); tips of toes strongly depressed and dilated, the inferior pad somewhat pointed distally and separated from the superior portion by a crescentic, dorsally subterminal groove; subarticular tubercles generally oval, more protrudent distally; metatarsal area covered with small tubercles; inner metatarsal tubercle elongate-elliptical, its length equal to or greater than its distance from the distal end of the subarticular tubercle of the inner toe; the outer moderate, round; toes generally webbed to the disk on the first and fifth and almost to the distal tubercle on the inside of the fourth; dorsum with small to moderate porous warts and tubercles, generally more numerous and larger posteriorly and on the hindlimbs, frequently in somewhat elongate folds on the upper lateral surfaces; posterior venter and lower surface of the thighs granulate.

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[1] M.C.Z. 7408 is recorded from Ugi Id. However, a note inserted in the body cavity at the time it was collected gives the station as Pamua which is on San Cristobal.

Color of the dorsum (in preservative) light-brown to dark reddish-brown, generally with lighter blotches anteriorly and often with small blackish, scattered blotches, and with narrow, dark, transverse bars on the hindlimbs; venter whitish to light-brown, diffused or marbled with darker brown on the head and pectoral areas.

Ovarian eggs are large and unpigmented.

Measurements	♂ (M.C.Z. 7412)	♀ (A.M.N.H. 35436)
Snout to vent	103 mm.	147 mm.
Snout length	17.5 "	25 "
Head length (to posterior edge of tympanum)	35 "	48 "
Head breadth	46 "	66 "
Eye diameter	11 "	16 "
Tympanum diameter	6 "	7 "
Tibia length	48 "	68 "

Range. (See distributional chart).

A single male specimen (A.M.N.H. 35421) from Kolombangara is generally smoother on the dorsum, has the webs of the toes much reduced (about 1/3 instead of 2/3 webbed) and has a larger tympanum in relation to the eye. This may represent a geographic race occupying this island or perhaps the New Georgia group if additional material shows these differences to be consistent.

Genus Palmatorappia Ahl

Ahl (1927, p. 113) set up this genus based on a re-examination of the type and paratypes of Sternfeld's *Hylella solomonis* which he found to belong to the Ranidae rather than the Hylidae. He at that time considered it to be near to *Hyperolius* (*Rappia* of authors). Noble (1931, p. 524) would derive *Palmatorappia* from *Cornufer* or an allied genus, stating that the omosternum is forked at the base. An examination of one of Sternfeld's paratypes (Senckenberg Museum, No. 6602) shows this to be true, and Ahl's statement (1927, p. 113), "*Omosternum mit knöchernem, ungegabelten Stiel*", is in error. As pointed out by Mertens (1929, p. 268) Kinghorn's (1928, p. 130) description of *Hypsirana,* based upon specimens of this Solomons frog, was published without knowledge of Ahl's or Sternfeld's earlier work.

The pupil is horizontal; vomerine teeth are absent; fingers and toes are almost fully webbed. In the only known species the tips of the fingers and toes are dilated into large, somewhat truncate disks. The inferior pad of the disk is separated from the superior portion by a crescentic groove which joins laterally with a ventral transverse groove forming the proximal boundary of the pad as in most species of *Cornufer*. The outer metatarsals are separated by a groove (not united as stated by Ahl, 1927, p. 113); the omosternal style is forked at the base; the terminal phalanx is T-shaped.

Palmatorappia solomonis (Sternfeld)

(Pl. 1, fig. 5; Pl. 5, fig. 3)

Hylella solomonis Sternfeld, 1920 (1921), Abhand. Senckenberg. Natur. Ges., 36, p. 436, Pl. xxxi, fig. 10: Buka Id. (Type in Senckenberg Museum).
Palmatorappia solomonis, Ahl, 1927, Sitz. Ges. Natur. Fr. Berlin, p. 114.
Hypsirana heffernani, Kinghorn, 1928, Rec. Austral. Mus. 16, p. 130, fig. 7: Tunabuli, Isabel Id. (Type in Australian Museum).

Description. Head broad, its breadth equal to or greater than its length, about 2/5 the length from snout to vent, 3/4 to 4/5 the length of the tibia; snout round, scarcely projecting beyond the lower jaw; eye large, its diameter more than 1/3 the breadth of the head; tympanum indistinct, round, its diameter about 1/2 that of the eye; interorbital space broader than the upper eyelid; loreal region nearly vertical, concave; canthus rostralis rounded; vomerine teeth absent; tongue small, oval with a shallow notch at the mid-point of the posterior free margin.

Forelimb well developed; fingers strongly depressed, first shorter than the second; tips dilated into large, distally rather truncate disks, the inferior pad of which is separated from the superior portion by a crescentic groove which is continuous laterally with a transverse groove across the ventral surface forming the proximal border of the disk as in *Cornufer*; pad transversely elliptical, disks scarcely broader than the subtending digit which is bordered laterally by a wide dermal flange as in *Hyla lutea*; subarticular tubercles very small, round or oval, scarcely protrudent; inner metacarpal tubercle small, elliptical, rather indistinct; outer large, round, indistinct; fingers webbed to the distal tubercle or nearly to the disk except for the third; hindlimb well developed; length of tibia half or more than half the length from snout to vent; toes depressed; tips dilated into large disks with inferior transversely elliptical pads limited as on the fingers; disks about the same size as those of the fingers, scarcely broader than the subtending digit which is bordered laterally by a wide dermal flange; subarticular tubercles small, oval, little protrudent; inner metatarsal tubercle broadly elliptical, rather indistinct, outer absent; toes webbed to the distal tubercle or nearly to the disk except the fourth and on the inner side of the third; dorsum on upper lateral surfaces smooth but with numerous small, round, rather colorless, depressed areas; lower lateral surfaces, venter posterior to the pectoral region and inferior surfaces of the thighs with large flat granules.

Color (in preservative) of the dorsum, as described by Kinghorn, is at first purplish-brown, gradually fading to yellowish, or greenish-olive. The venter is yellowish.

Small ovarian eggs are unpigmented.

Measurements	(Senckenberg Museum 6602)
Snout to vent	28 mm.
Snout length	4 "
Head length (to posterior edge of tympanum)	10 "
Head breadth	11 "
Eye diameter	4 "
Tympanum diameter	2 "
Tibia length	15 "

Range. Known from Buka and Isabel Islands.

Genus PLATYMANTIS Günther

In general agreement with Boulenger (1918b, p. 372) and Deckert (1938, p. 148) the genus *Platymantis* may be defined as follows: ranids possessing small or moderate disks on the tips of the toes and fingers (or tips of fingers may be simply swollen in some species, as *P. solomonis* for example); a distinct ventral pad present on the disks of the toes, often also of the fingers, separated from the dorsal part by a crescentic groove on the distal and lateral margins; toes free or occasionally with basal webs; terminal phalanx bluntly rounded; outer metatarsals united; omosternal style broadly forked at the base. Fully developed eggs are large and unpigmented for all species where such uterine or ovarian eggs are known.

The following key applies to the species known from the Solomon Islands:

1. First and second fingers of about equal length or first but slightly longer . . 2
   First finger much longer than second 3
2. Tips of fingers dilated into moderate, depressed disks with ventral pad separated from the dorsal part by a deep crescentic groove . . . . . . *myersi*
   Tips of fingers undilated, pointed, without a groove separating the ventral from the dorsal portions . . . . *aculeodactylus sp. nov.*
3. Tips of fingers slightly dilated and depressed with dorsal and ventral parts separated by a short, terminal crescentic groove (most prominent in males); dorsum rugose with folds moderately long and narrow; length of tibia generally greater than one-half the length from snout to vent . . . . . *papuensis weberi*
   Tips of fingers simply swollen without a groove separating ventral and dorsal portions; dorsum nearly smooth or moderately rugose with short relatively wide folds; length of tibia generally less than one-half the length from snout to vent . . . . *solomonis*

PLATYMANTIS ACULEODACTYLUS sp. nov.

(Pl. 5, fig. 1)

Two specimens from Torokina area, Bougainville Island, which were collected by W. L. Necker and D. H. Johnson in 1944–45, represent a very diminutive and until now undescribed species of this genus. A 25 mm. female is mature, whereas females of the other species of *Platymantis* known from the Solomons do not become mature until they have reached a length of 50 to 60 mm. or more.

Type. Mature female (U.S.N.M. 119769).

Paratype. Juvenile (U.S.N.M. 119580).

(?)1 (A.M.N.H. 34733) Choiseul. (Whitney Exped.).

Definition. A very small *Platymantis* (the type measuring 25 mm. from snout to vent, possesses well developed oviducts and moderate sized, unpigmented, ovarian eggs) having a rather smooth skin; undilated, somewhat pointed finger tips; very large, nearly transverse vomerine tooth patches posterior to the choanae; tongue feebly indented at the mid-point of the posterior free margin. This species is apparently most closely related to *P. cheesmanae* Parker (1940, p. 257) from which it differs in the much larger vomerine tooth patches; greater length of the first finger, as long or longer than the second (not shorter); the greater breadth of the interorbital space, broader than the upper eyelid (not narrower).

Description of the type. Head moderately broad, about 2/5 the length from snout to vent and 4/5 the length of the tibia; snout rounded, its length about equal to the diameter of the eye; nostril nearer the tip of snout than eye; eye large, its diameter 1/3 or more the breadth of the head; interorbital space broader than the upper eyelid, less than the distance between the external nares; tympanum round, its diameter about 1/5 the breadth of the head; supratympanic fold moderate; canthus rostralis rounded; loreal region moderately oblique and concave; tongue broadly oval with a wide, shallow groove at the midpoint of the posteriorly free margin; vomerine teeth in two large, nearly transverse patches behind the levels of the choanae, extending outward beyond the sagittal plane of the inner border of the choana on either side, the distance separating the patches much less than the length of either.

Forelimb well developed; first, second and fourth fingers about equal in length; fingers pointed at tips, not dilated, without a groove separating the superior and inferior portions; subarticular tubercles large (except the distal one of the third finger), round to oval, only moderately protrudent; basal ones smaller and narrower; inner metacarpal tubercle very large, broadly oval, nearly in contact with the basal tubercle of the first finger; middle one of equal length but narrower; outer short, elliptical; terminal phalanx bluntly rounded; fingers without webs; hindlimb moderately long, length of tibia about 1/2 the length from snout to vent, heel reaching the anterior corner of the eye; toes long, in order of length 1, 2, 5, 3, 4; tips dilated into moderate, pointed disks with a deep, almost angular groove separating the dorsal and ventral portions; subarticular tubercles moderate, round to oval, more strongly protrudent than those of the fingers; inner metatarsal tubercle narrow-elliptical, its length greater than its distance from the distal end of the tubercle of the first toe, outer relatively large, round, metatarsal area smooth; toes without webs; dorsum nearly smooth except for two or three short, indistinct, light folds on either side on the pectoral and dorsolateral area and scattered fine tubercles posteriorly; upper lateral surfaces and inner proximal region of the thighs finely tuberculate; venter smooth.

Color (in preservative) of the dorsum and upper lateral surface purplish-brown with darker blotches in the middorsal area and enclosing the few light-colored folds; a wide, purplish-gray dorsolateral stripe extending posteriorly from either eye; loreal regions very dark;

margin of lips with wide, irregular, very dark, transverse bars; upper surfaces of limbs with broad, dark blotches or transverse bands; inner surface of thighs dark in the anal region, lightly speckled with purplish-brown distally; venter very light except for the dark blotches along the margin of the lower jaw.

Measurements	♀ (U.S.N.M. 119769)
Snout to vent	25 mm.
Snout length	3.5 "
Head length (to posterior edge of tympanum)	10 "
Head breadth	10.5 "
Eye diameter	3.5 "
Tympanum diameter	2 "
Tibia length	13 "

The paratype, a 16 mm. juvenile, has the same dorsal color pattern but is lightly speckled with reddish-brown on the venter anterior to the forelimb.

A third specimen, a 26 mm. female from Choiseul (A.M.N.H. 34733)[1], is also referred to this species. It agrees very well in the pointed fingers and toes, and the small size, but differs in the broader head, greater rugosity of the dorsum, large granules of the posterior venter and thighs and lack of the light-colored dorsolateral bands. The vomerine teeth are also smaller.

PLATYMANTIS MYERSI Brown

(Pl. 4, fig. 3; Pl. 8, fig. 2)

Rana solomonis (part), Burt and Burt, 1932, p. 491.

Platymantis myersi Brown, 1949, Amer. Mus. Nov., No. 1387: Bougainville Id. (Type in American Museum of Natural History).

2 (A.M.N.H. 35340, 35348, holotype) Bougainville Id. (Whitney Exped.).
1 (S.N.H.M. 9334) Bougainville Id. (Exch. Amer. Mus.) 1948.
1 (U.S.N.M. 119584) Torokina, Bougainville Id. (W. L. Necker).

In describing this species I suggested that it might be most nearly related to *P. vitianus*, but later work with members of this genus suggests probable closer affinities with *P. beauforti*.

Description. Head moderately broad; its breadth slightly less than its length, less than 3/4 the length of the tibia; snout relatively pointed, projecting beyond the lower jaw; eye large, its diameter about 1/3 the breadth of the head; nostril nearer tip of snout than eye; interorbital space much narrower than the upper eyelid; tympanum, covered with a thin skin, vertically oval, its diameter less than 1/5 the breadth of the head; vomerine teeth in two short, slightly oblique patches, the anterior vortex of the triangular bases between the choanae, the toothed crests behind the level of the choanae; tongue rather narrow, oval with a deep notch at the mid-point of the posterior border.

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[1] Burt and Burt (1932, p. 491) include this specimen in their list referred to *Rana solomonis*.

Forelimbs well developed; fingers long, the first and second approximately equal in length; the tips of the fingers expanded into distinct, round disks whose breadth is about 1½ times that of the adjacent phalanx, depressed with inferior pad separated from the superior portion by a deep, terminal, crescentic groove; subarticular tubercles large (except for the basal ones which are small, oval), round or broadly oval, only moderately protrudent; inner metatarsal tubercle prominent, elliptical, its length about equal to its distance from the mid-point of the distal subarticular tubercle of the first finger, middle one rather large, round or oval, outer moderate, narrow-elongate; hindlimb long, the length of the tibia more than 1/2 the length from snout to vent; toes long, slender, webbed at base; tips dilated, rounded, depressed with inferior pads separated from the superior part by a crescentic, dorsally subterminal groove; subarticular tubercles moderate, oval, distally pointed, inner metatarsal tubercle narrow, elongate, its length equal to its distance from the distal end of the subarticular tubercle of the first toe, outer distinct, small, round; metatarsal area slightly granulate or almost smooth.

Dorsum with only a few scattered swollen areas (except the posterior part which shows some tubercles as does the posterior part of the upper eyelids); lateral surfaces granulate and with short folds and tubercles, posterior venter and posterior aspect of thighs finely granulate.

Color of dorsum (in preservative) mottled dark grayish-brown with a somewhat indistinct darker brown blotch in the interorbital area; lateral surfaces and limbs browner; hands and feet dark grayish-brown; lips with three broad, dark-brown transverse bands which taper dorsally; venter more grayish than dorsum but heavily marbled with dark reddish-brown.

A small juvenile (U.S.N.M. 119584), which I refer to this species, measures 14.25 mm. from snout to vent. The body and limbs are slender. The fingers and toes are not dilated at the tips in this early juvenile stage but bluntly rounded. The venter is very dark, heavily mottled with brown as in the adult. The vomerine teeth, however, are quite inconspicuous although very prominent in the adult.

Measurements	♂ (S.N.H.M. 9335)	♀ (A.M.N.H. 35348)
Snout to vent	55 mm.	58 mm.
Snout length	9.5 "	11 "
Head length (to base of skull)	19 "	19.25 "
Head breadth	20.5 "	22.5 "
Eye diameter	7 "	8 "
Tympanum diameter	3 "	3.5 "
Tibia length	29 "	31 "

Range. Known at present only from Bougainville Island.

PLATYMANTIS PAPUENSIS WEBERI Schmidt

(Pl. 1, fig. 3; Pl. 4, fig. 4)

Platymantis solomonis (part), Barbour, 1921, p. 96.
Rana solomonis (part), Burt and Burt, 1932, p. 491.
Platymantis weberi Schmidt, 1932, Field Mus. Nat. Hist. Zool. Series, 18, p. 178: Tulagi Id., Solomon Ids. (Type in Chicago Natural History Museum).

17 (M.C.Z. 7487–96, 7498–99, 7501–04 + 1 uncat.) Tulagi Id. (W. M. Mann) 1916.
22 (M.C.Z. 7552–53, 7555–73, 7575) Isabel Id. (W. M. Mann) 1916.
4 (" 7582–84, 7587) Malaita Id. " "
3 (C.A.S. 49951, 49954–55) Guadalcanal Id. (J. A. Kusche) 1920.
1 (" 54667) Isabel Id. (Exch. Mus. of Comp. Zool.).
1 (S.N.H.M. 9341) Guadalcanal Id. (Exch. Amer. Mus. Nat. Hist.) 1948.
1 (S.N.H.M. 9340) Bougainville Id. (Exch. Amer. Mus. Nat. Hist.) 1948.
1 (A.M.N.H. 22857) Vangunu Id. (Whitney Exped.).
6 (A.M.N.H. 34258, 35303–05, 35328–29) Bougainville Id. (Whitney Exped.).
1 (A.M.N.H. 35396) Narovo Id. (Whitney Exped.).
1 (" 35439) Vella Lavella Id. " "

Schmidt (1932, p. 178) in describing *P. weberi* noted as distinctive characteristics its small size (based on males only), the shortness of the patches of vomerine teeth, the relatively acute snout, presence of numerous elongate dorsal folds and the presence of a terminal, crescentic, horizontal groove separating the inferior and superior portions of the slightly expanded disks at the tips of the fingers. He also stated that he regards Boulenger's reference (1888a, p. 90) of specimens from New Georgia and Guadalcanal Islands to *P. corrugatus* as being based on material of this species.

Actually *P. weberi* is much more closely related to *P. papuensis* (Meyer, 1874) of New Guinea from which it appears to differ in the presence of a more distinct inner tarsal fold, more prominent and slightly wider folds on the dorsum; the greater rugosity of the solar area and the generally more distinct groove separating the inferior and superior portions of the minute disks of the finger. The folds on the dorsum of both these forms are like those of *P. corrugatus* but shorter and more numerous. The latter is a broader-headed species with hindlimbs longer and eyes smaller as noted by Loveridge (1948, p. 407). Close comparative examination of a series of these three populations leads one to conclude that *P. corrugatus* is a distinct species and that *P. papuensis* and *P. weberi* probably represent geographically isolated and subspecifically differentiated populations of the same species.

The significance of the differences between the means of various measurements of the populations concerned is summarized in the following tables.

	Mean of snout to vent length (in mm.)					
	Male	Female	diff.	t	n	P
Platymantis papuensis papuensis Hollandia area, Dutch New Guinea	($N_1 = 11$) 37.5 ±.42	($N_2 = 9$) 51.67 ±1.08	14.17	13.12	18	highly significant
Platymantis papuensis weberi Isabel Id., Solomons	($N_1 = 7$) 36.86 ±1.05	($N_2 = 13$) 49.31 ±1.08	12.45	7.45	18	highly significant

	P. p. papuensis Dutch New Guinea ($N_1 = 20$)	*P. p. weberi* Isabel Id. ($N_2 = 19$)	diff.	t	n	P
$\frac{\text{Breadth of head}}{\text{Length snout to vent}}$	38.20 ± .29	38.48 ± .20	0.19	0.54	37	$> .5$
$\frac{\text{Breadth of head}}{\text{Length of tibia}}$	73.82 ± .96	76.14 ± .70	2.30	1.918	37	$> .05$
$\frac{\text{Length of tibia}}{\text{Length snout to vent}}$	52.34 ± .53	50.67 ± .39	1.67	2.506	37	$< .02$

Both populations exhibit a pronounced sexual dimorphism when snout to vent lengths for males and females are compared; the difference between the means in either case is highly significant. The males are much smaller than the females.

There is no significant difference in body proportions, except perhaps for the length of the tibia in relation to the snout to vent length, between New Guinea and Solomons populations.

Description. Head slightly less broad than long; its breadth generally less than 2/5 the length of the body (38.48% ± .20 for 19 specimens from Isabel Island), about 3/4 the length of the tibia (76.14% ± .70 for 19 specimens); snout round-pointed, relatively more pointed than for *P. solomonis*; nostril nearer tip of snout than eye; eye moderately large, its diameter about 1/3 the breadth of the head (33.71% ± .364 for 19 specimens); interorbital space less than the breadth of the upper eyelid; tympanum large, its diameter generally about 1/5 the breadth of the head (22.56% ± .625 for 19 specimens); vomerine teeth in two short, rather widely separated, oblique patches generally posterior to the choanae; tongue moderate, oval with a rather wide, deep notch at the mid-point of the free, posterior margin.

Forelimb well developed; first finger longer than the second; finger tips slightly dilated, usually somewhat depressed with a shallow but generally distinct, terminal, crescentic groove separating the inferior and superior parts of the disk at the distal and lateral margins; subarticular tubercles other than the basal ones large, round, about as broad as the subtending digit, strongly protrudent and tending to be pointed distally; basal ones smaller, round, weakly protrudent; inner metacarpal tubercle broadly elliptical, its length about equal to its distance from the distal tubercle of the first finger; middle one shorter, broadly oval; outer much shorter, oval or elliptical; hindlimb moderate, length of tibia about 1/2 the length of the body (50.67% ± .39 for 19 specimens); tips of toes moderately dilated, depressed, the inferior pad of the disk separated from the superior part by a deep, terminal, crescentic groove; subarticular tubercles round to broadly oval, strongly protrudent and pointed distally; solar area prominently tuberculate; inner metatarsal tubercle moderately broad, elliptical, its length about equal to its distance from the distal end of the tubercle of the first toe; outer moderate, round, strongly protrudent; a low tarsal fold extending proximally from the base of the inner metatarsal tubercle; toes without webs; dorsum with short to moderate, narrow folds generally displaying a pattern of about eight longitudinal rows anteriorly and diminishing posteriorly; rugose with small tubercles between the folds of the dorsum, the upper eyelids, loreal areas, upper lateral surfaces and the upper proximal surfaces of the hindlimbs;

lower abdomen and posterior thighs with moderate flat granules; under surface of head of males generally finely granulate.

Color (in preservative) of the dorsum light-brown to dark reddish-brown, often with darker blotches and dark interorbital bar, frequently with a wide purplish-gray dorsolateral band on each side, occasionally with bright red markings in association with some of the folds and tubercles on dorsum and limbs; margins of lips with more or less distinct, irregular transverse, dark bars; loreal region sometimes very light; upper surface of thighs and tibial region with wide, dark transverse bars or blotches; venter uniformly light or more or less powdered or marbled with brown anterior to the forelimbs.

Ovarian eggs are large and unpigmented.

Measurements	♂ (M.C.Z. 7562)	♀ (M.C.Z. 7560)
Snout to vent	40 mm.	56 mm.
Snout length	7 "	10 "
Head length (to posterior edge of tympanum)	16 "	22 "
Head breadth	15 "	21 "
Eye diameter	5 "	8 "
Tympanum diameter	4 "	4 "
Tibia length	19 "	27 "

Range. (See distributional chart).

PLATYMANTIS SOLOMONIS (Boulenger)

(Pl. 1, fig. 4; Pl. 2, fig. 1; Pl. 4, fig. 1)

Cornufer solomonis Boulenger, 1884, Proc. Zool. Soc. London, p. 212: Fauro, Treasury and Shortland Ids. (Type in British Museum).
Platymantis solomonis, Boulenger, 1918b, p. 372.
Platymantis solomonis (part), Barbour, 1921, p. 96.
Rana solomonis (part), van Kampen, 1923, pp. 191–192.
Rana solomonis (part), Burt and Burt, 1932, p. 491.

1 (M.C.Z. 3499) Stirling Id. (Exch. Brit. Mus.).
3 (" 7444, 7554, 7561) Isabel Id. (W. M. Mann) 1916.
2 (" 7497, 7500) Tulagi Id. " 1916.
1 (" 7581) Malaita Id. " 1916.
2 (" 7585–86) New Georgia Id. " 1916.
6 (" 26085–89 — 1 uncat.) Stirling Id. (L. W. Jarcho) 1945.
1 (" 72080) New Georgia Id. (Crocker Exped.) 1933.
2 (M.V.Z. 44948–49) Munda, New Georgia Id. (C. G. Sibley) 1944.
1 (S.N.H.M. 8393) Torokina Pt., Bougainville Id. (J. P. Heath) 1943.

12 (U.S.N.M. 119590–93, 119776–81) Torokina Pt., Bougainville Id. (W. L. Necker and D. H. Johnson).
1 (U.S.N.M. 119594) Puruata Id.
18 (A.M.N.H. 34257, 35259–60, 35306, 35308–11, 35314–15, 35317, 35320–26) Bougainville Id. (Whitney Exped.).
1 (A.M.N.H. 22856) Vangunu Id. (Whitney Exped.).
1 (" 35386) Arnavon Id. " "
1 (" 35389) Choiseul Id. " "
1 (" 35391) Mono Id. " "
1 (" 39997) Malaita Id. " "

Boulenger (1884, p. 212) based his description on specimens from the small islands near the southern end of Bougainville, noting such characteristics as the large head and eyes, tips of fingers swollen rather than dilated, interorbital distance less than breadth of upper eyelid, and dorsal surfaces slightly rugose with short longitudinal folds. His figure (1886, pl. xi, fig. 2) well illustrates this large eyed, moderately or but slightly rugose species which is widely distributed in the Solomons. This very large species may have its closest affinities with *P. vitianus*.

Subspecific populations are very strongly suggested when series from different island groups are carefully examined. However, since the only samples available containing five specimens or more, of either sex are those from Bougainville, Stirling and New Georgia Islands, no well defined geographical limits can be determined for the suggested subspecies. Consequently no predictions are made at this time.

Description. Head about as broad as long; its breadth almost 2/5 the length from snout to vent (37.77% ± .434 for 11 specimens from Bougainville Island), 3/4 to 4/5 the length of the tibia (77.19% ± .908 for 11 specimens); snout round or round-pointed, only slightly protrudent beyond the lower jaw; nostril nearer tip of snout than eye; eye large, its diameter more than 1/3 the breadth of the head (37.37% ± .555 for 11 specimens), tympanum round, large, its diameter about 1/5 to 1/4 the breadth of the head; vomerine teeth in two strongly protrudent, oblique or transverse patches with the crests posterior to the choanae and the outer angle of the bases extending outward beyond the sagittal plane of the inner border of the choana or either side, the distance separating the patches slightly more or less than the length of either; tongue rather broadly oval with a narrow to broad cleft at the mid-point of the posterior free margin.

Forelimb well developed, first finger longer than the second; tips of fingers swollen and not or scarcely dilated, without a groove separating inferior and superior portions; subarticular tubercles large, distal ones about as broad as the subtending digit; round or somewhat oval, strongly protrudent; inner metacarpal tubercle broadly elliptical, its length about equal to its distance from the subarticular tubercle of the first finger; middle one broadly oval, shorter; outer narrower; hindlimb moderately long; length of tibia about 1/2 the length from snout to vent (49.79% ± .513 for 11 specimens); tips of toes dilated into small disks, the inferior portion separated from the superior by a crescentic, terminal groove; subarticular tubercles oval, smaller than on hands, strongly protrudent and pointed distally; solar area strongly tuberculate; inner metatarsal tubercle narrow elliptical, its length equal to its distance from the distal end of the tubercle of the first toe; outer round, strongly protrudent; toes without webs; dorsum only moderately rugose with scattered, short, relatively broad folds or tubercles, very nearly smooth for larger, older females; lateral surfaces granulate or with some tubercles; venter granulate posteriorly and on the inner surface of the thighs.

Color (in preservative) of the dorsum grayish-brown to reddish-brown or blackish-brown often with darker blotches; limbs often lighter; thighs and tibial regions with more or less distinct, wide, transverse bars or blotches; margin of lips with more or less distinct, broad, dark transverse bars; lower lateral surfaces lighter, powdered or marbled with darker shades; venter white, grayish or pale-brown posteriorly, generally powdered or marbled with brown or reddish-gray anterior to the forelimbs.

Ovarian eggs are large and unpigmented.

Measurements	♂(U.S.N.M. 119392)	♀(U.S.N.M. 119591)
Snout to vent	49 mm.	66 mm.
Snout length	9 "	11 "
Head length (to posterior edge of tympanum)	20 "	26 "
Head breadth	18 "	25.5 "
Eye diameter	7 "	9 "
Tympanum diameter	4 "	4 "
Tibia length	25.5 "	31 "

Range. (See distributional chart).

Genus RANA Linné

The genus *Rana* is represented in the Solomon Islands by two known populations of the subgenus *Hylarana*. *Rana papua krefftii* occupies only the extreme southwestern islands of the San Cristobal group. The subspecies represented in the other groups, so far as known, is here referred to *Rana papua novaebritanniae*, although subspecific identity of the Bismarcks and northern Solomons populations may be shown to be in error when a large number of specimens from the former locality become available for comparison.

Some of the specimens in the limited collections from Guadalcanal and Malaita which I have been able to examine are somewhat intermediate between these two populations. However, since they agree in most characteristics with *R. papua novaebritanniae*, I have assigned them here until such time as more material is available from these island groups as well as the interlying Choiseul and Isabel groups.

These two subspecies may be distinguished as follows:

Tympanum large, its diameter more than 1/4, generally more nearly 1/3 the breadth of the head; disks of toes small, oval; snout generally rounded, little protrudent; venter whitish or light, not or little mottled with blotches of brown . . . . *papua novaebritanniae*

Tympanum moderate, its diameter generally less than 1/4 the breadth of the head; disks of toes moderate, somewhat pointed; snout moderately pointed, generally protrudent; venter usually mottled with large brown blotches . . . *papua krefftii*

RANA PAPUA KREFFTII Boulenger

(Pl. 6, fig. 1)

Hylarana erythraea (part), Günther, 1858, p. 73.
Rana krefftii Boulenger, 1882, Cat. Batr. Sal. Brit. Mus., p. 64, pl. iii, fig. 2: San Cristobal Id. (Type in British Museum).
Rana (*Hylarana*) *krefftii* (part), Boulenger, 1918a, pp. 239–41.
Rana krefftii (part), Barbour, 1921, pp. 97–98.
Rana kreffti (part), van Kampen, 1923, pp. 206–07.
Rana krefftii (part), Kinghorn, 1928, pp. 125–26.

1 (M.C.Z. 2517) Solomon Ids. (W. M. Mann) 1916.
46 (" 7432–34, 7505–47) Bio Id. " "
1 (" 7440) San Cristobal Id. " "
1 (" 7447) Santa Ana Id. " "
4 (U.S.N.M. 63402–05) Bio Id. " "
1 (C.A.S. 54666) San Cristobal Id. " "

Boulenger (1882, p. 64) described *R. papua krefftii* on the basis of two specimens, one from San Cristobal Island and one with the more general locality designation of Solomon Islands. In view of the fact that well differentiated subspecies occupy different geographical areas within the Solomon Islands, I designate San Cristobal as the type locality of *R. papua krefftii*.

Description. Head less broad than long, its breadth about 1/3 the length from snout to vent (34.75% ± .34 for 5 specimens from Bio and San Cristobal), about 2/3 the length of the tibia (66.43% ± 1.44 for 5 specimens); snout pointed, generally strongly protrudent beyond the lower jaw; nostril nearer tip of snout than eye; eye moderate, its diameter 1/3 to about 2/5 the breadth of the head (36.8% ± 1.136 for 5 specimens); tympanum moderate, its diameter generally less than 1/4 the breadth of the head (22.02% ± .277 for 5 specimens); interorbital space less than, or equal to, the breadth of the upper eyelid; loreal region nearly vertical, concave; canthus rostralis angular; vomerine teeth in two oblique patches between the choanae, the distance separating them generally less than the length of either; tongue oval with a moderate to broad, rounded notch at the mid-point of the posterior, free margin.

Forelimb well developed; fingers long, slender, the first longer than the second; tips dilated into somewhat pointed disks nearly as large as those of the toes, a rather angular groove (frequently incomplete at the vertex) separating the distally narrower, inferior pad from the superior portion; subarticular tubercles round or broadly oval, generally more protrudent distally, nearly as broad as the subtending digit (except the basal ones which are low and somewhat narrow elliptical); inner metatarsal tubercle broadly elliptical, its length less than its distance from the distal end of the distal tubercle of the inner finger; middle one shorter, broadly oval, outer narrow elliptical; fingers without webs; males with a prominent humeral gland; hindlimb long; length of tibia about 1 2/5 to slightly more than 1 1/2 times the breadth of the head; toes long; tips dilated into moderate, somewhat pointed disks, the inferior pad separated from the superior portion by a deep, distally complete, somewhat angular groove; subarticular tubercles small, narrow elliptical, its length less than its distance from the subarticular tubercle of the inner toe; outer one small, round; toes webbed to the distal tubercle or almost the disk except the fourth which is webbed only to the penultimate or occasionally the distal tubercle on the inside; outer metatarsals separated to base; a distinct outer metatarsal fold present; skin of the dorsum generally rather smooth; upper surfaces of the limbs with very fine longitudinal folds; lateral surfaces nearly smooth or moderately granulate; venter nearly smooth or finely granulate posteriorly; inferior and inner surfaces of the thighs granulate at least proximally.

Color (in preservative) of dorsum reddish-brown, occasionally olive-brown, but generally lighter than for *R. papua novaebritanniae*; lateral surfaces of head and upper lateral surfaces of body dark reddish-brown to almost blackish-brown, bordered ventrally by a narrow light band beginning anteriorly at the angle of the jaws; lower lateral surfaces mottled with brown; margin of lips generally suffused with brown; upper surface of limbs lighter to same color as the dorsum, thigh and lower leg barred or irregularly blotched with dark-brown; venter, especially on the head and throat, heavily blotched with brown, or occasionally only retaining the dark-brown on the ventral margin of the lower jaw and the pectoral blotches.

Ovarian eggs small and heavily pigmented at the animal pole region.

Measurements	♂ (M.C.Z. 7533)	♀ (C.A.S. 54666)
Snout to vent	52 mm.	82 mm.
Snout length	8 "	13.5 "
Head length (to posterior edge of tympanum)	20 "	32 "
Head breadth	17 "	29 "
Eye diameter	5 "	10.75 "
Tympanum diameter	4.5 "	6.5 "
Tibia length	27 "	41 "

Range: (See distributional chart).

RANA PAPUA NOVAEBRITANNIAE Werner

(Pl. 6, fig. 4)

Rana novaebritanniae Werner, 1894, Zool. Anz., 17, p. 155: New Britain. (Type in Berlin).
Rana (*Hylarana*) *krefftii* (part), Boulenger, 1920, pp. 186–88.
Rana papua, Sternfeld, 1920 (1921), p. 433.
Rana krefftii (part), Barbour, 1921, pp. 97–98.
Rana kreffti (part), van Kampen, 1923, pp. 206–07.
Rana krefftii (part), Kinghorn, 1928, pp. 125–26.
Rana krefftii, Schmidt, 1932, p. 180.
Rana kreffti (part), Hediger, 1934, pp. 451, 486.
Rana krefftii, Slevin, 1934, p. 184.

2 (M.C.Z. 7442–43) Isabel Id. (W. M. Mann) 1916.
2 (" 7445–46) Tulagi Id. " "
(?)1 (" 7448) Santa Cruz Id.[1] " "
15 (U.S.N.M. 119611–23, 119774–75) Torokina, Bougainville Id. (W. L. Necker).
2 (M.V.Z. 44192, 44222) Guadalcanal Id. (J. Chattin) 1944.
5 (C.A.S. 72076–79, 72166) Malaita Id. (Crocker Exped.) 1933.

Description. Head less broad than long, its breadth about 1/3 the length from snout to vent (33.67% ± .318 for 15 specimens from Bougainville Island) and about 2/3 the length of the tibia (67.65% ± .984 for 15 specimens); snout round-pointed, little protrudent; nostril nearer tip of snout than eye; eye large, its diameter about 2/5 to nearly 1/2 the breadth of the head (40.74% ± .759 for 15 specimens); tympanum large, round, its diameter 1/4 to 1/3 the breadth of the head (31.93% ± .617 for 15 specimens); interorbital distance less than the breadth of the upper eyelid; loreal region nearly vertical, somewhat concave; canthus rostralis rather angular; vomerine teeth in two short, oblique patches between the choanae, the distance separating them less than the length of either; tongue generally narrow-oval with a deep, narrow, rounded notch at the mid-point of the free posterior margin.

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[1] Exact locality for this specimen is in doubt; it is almost certainly some other island.

Forelimb well developed; fingers long, the third finger longer than the snout, first longer than the second; tips of fingers dilated into moderate, oval or slightly pointed disks about the same size as those of toes, with a prominent terminal, semicircular groove separating the inferior pad from the superior portion; subarticular tubercles large, oval; inner metacarpal tubercle elliptical, about twice as broad as long, its length equal to its distance from the distal end of the tubercle of the inner finger; middle one shorter, almost as broad as long; outer short and narrow; fingers without webs; male generally with humeral gland present; hindlimb long; heels moderately overlapping when the hindlimbs are placed at right angles to the body; heel of the appressed limb reaching the loreal region; length of tibia about 1/2 the length from snout to vent (49.97% ± .577 for 15 specimens); tips of toes dilated into moderate, oval disks, the inferior pad less broad than the superior portion and separated from it by a semicircular groove as in the fingers; subarticular tubercles small, oval, more strongly protuberant distally; inner metatarsal tubercle elliptical-elongate, 2 to 2½ times as long as broad, shorter than its distance from the distal end of the subarticular tubercle of the inner toe, outer moderate, round; toes webbed to a point between the distal tubercle and the disk except for the fourth and the third on the inside where the web reaches the penultimate tubercle or beyond; skin of the dorsum almost smooth or finely granulate posteriorly; venter smooth; proximal region of the posterior surface of the thighs and anal area granulate.

Color (in preservative) of the dorsum dark-reddish or grayish-brown, raised tubercles, where present, darker; upper lateral surfaces of head and body blackish-brown, bordered dorsally by the moderately narrow, light dorsolateral fold; white or dusky gray coloration of upper lip continuous with the narrow, light stripe along the upper lateral surface from the angle of the jaw to the groin; lower lip white or dusky; venter white or occasionally powdered with brown or gray anteriorly; upper surface of limbs grayish or brown; lighter than body; thigh and lower leg with broad, dark transverse bars; posterior thighs mottled with blackish-brown; a large brown blotch on the outer inferior surface of the upper arm; lower thighs whitish or somewhat mottled with grayish-brown; under surface of hands and feet grayish-brown.

Ovarian eggs are small and darkly pigmented in the animal pole region.

Measurements	♂ (U.S.N.M. 119611)	♀ (U.S.N.M. 119616)
Snout to vent	50 mm.	51 mm.
Snout length	8 "	8.25 "
Head length (to posterior edge of tympanum)	20 "	20 "
Head breadth	18.5 "	17 "
Eye diameter	7 "	7 "
Tympanum diameter	5 "	5 "
Tibia length	25 "	26 "

Range. (See distributional chart).

BIBLIOGRAPHY

Ahl, Ernst

1927. Ueber neue oder seltene Froschlurche aus dem Zoologischen Museum Berlin. Sitz.-Ber. Ges. Naturf. Freunde, Berlin, Jahrg. 1926, pp. 111–117.

Barbour, Thomas

1912. A Contribution to the Zoögeography of the East Indian Islands. Mem. Mus. Comp. Zoöl., **44**, pp. 1–205, pls. i–viii.

1921. Reptiles and Amphibians from the British Solomon Islands. Proc. New England Zool. Club, **7**, pp. 91–122, pls. ii–iv.

Boulenger, G. A.

1882. Catalogue of the Batrachia Salientia s. Ecaudata in the Collection of the British Museum. (ed. 2, London), pp. xvi+503, text figs., pls. i–xxx.

1883. Descriptions of New Species of Reptiles and Batrachians in the British Museum. Ann. Mag. Nat. Hist. (5), **12**, pp. 161–167, pl. v.

1884. Diagnosis of New Reptiles and Batrachians from the Solomon Islands, collected and presented to the British Museum by H. B. Guppy, Esq. Proc. Zool. Soc. London, **1884**, pp. 210–213.

1886. On the Reptiles and Batrachians of the Solomon Islands. Trans. Zool. Soc. London, **12**, pp. 35–62, pls. vii–xiii.

1887. Second Contribution to the Herpetology of the Solomon Islands. Proc. Zool. Soc. London, **1887**, pp. 333–338, pl. xxviii.

1888a. Third Contribution to the Herpetology of the Solomon Islands. Proc. Zool. Soc. London, **1888**, pp. 89–90.

1888b. Note on the Classification of the Ranidae. Proc. Zool. Soc. London **1888**, pp. 204–206.

1890. Fourth Contribution to the Herpetology of the Solomon Islands. Proc. Zool. Soc. London, **1890**, pp. 30–31, pl. ii.

1910. Les Batraciens et Principalement Ceux d'Europe. (Paris), pp. 1–305, 55 figs.

1918a. On the Papuan, Melanesian, and North-Australian Species of the Genus *Rana*. Ann. Mag. Nat. Hist. (9), **1**, pp. 236–242.

1918b. Remarks on the Batrachian Genera *Cornufer* Tschudi, *Platymantis* Günther, *Simomantis*, g.n., and *Staurois* Cope. Ann. Mag. Nat. Hist. (9), **1**, pp. 372–375.

1920. A Monograph of the South Asian, Papuan, Melanesian, and Australian Frogs of the Genus *Rana*. Rec. Indian Mus., **20**, pp. 1–226.

Brown, W. C.

1949. A New Frog of the Genus *Platymantis* from the Solomon Islands. Amer. Mus. Novit., no. **1387**, pp. 1–3.

Brown, W. C., and Myers, G. S.

1949a. A New Frog of the Genus *Cornufer* from the Solomon Islands, with Notes on the Endemic Nature of the Fijian Frog Fauna. Amer. Mus. Novit., no. **1418**, pp. 1–10.

1949b. A New Frog of the Genus *Batrachylodes* from the Solomon Islands. Jour. Washington Acad. Sci., **39**, no. 11, pp. 379–380.

BURT, C. E., and BURT, M. D.

1932. Herpetological Results of the Whitney South Sea Expedition. VI. Bull. Amer. Mus. Nat. Hist., **63**, pp. 461–597, 38 figs.

CHUBB, L. J.

1934. The Structure of the Pacific Basin. Geol. Mag., **71**, pp. 289–302, 4 figs.

DARLINGTON, P. J., JR.

1948. The Geographical Distribution of Cold-blooded Vertebrates. Quart. Rev. Biol., **23**, no. 1, pp. 1–26; no. 2, pp. 105–123.

DECKERT, KURT

1938. Beiträge zur Osteologie und Systematik ranider Froschlurche. Sitz.-Ber. Ges. Natur. Freunde, Berlin, Jahrg. 1938, pp. 127–184, 49 figs.

DUMÉRIL, A.

1853. Mémoire sur les Batraciens Anoures, de la Famille des Hylaeformes ou Rainettes. Ann. Sci. Nat. (Paris), (3), **19**, pp. 135–179.

GIRARD, CHARLES

1853. Descriptions of New Species of Reptiles, Collected by the U. S. Exploring Expedition, under the Command of Capt. Charles Wilkes, U.S.N., 2nd Part — including Species of Batrachians, Exotic to North America. Proc. Acad. Nat. Sci. Philadelphia, **6**, pp. 420–424.

GÜNTHER, ALBERT

1858. Catalogue of the Batrachia Salientia in the British Museum. (London), pp. i–xvi+160, pls. i–xii.

GUPPY, H. B.

1887a. The Solomon Islands and their Natives. (Swan Sonnenschein, Lowrey and Co., London), pp. xvi+384.

1887b. The Solomon Islands, their Geology, General Features, and Suitability for Colonization. (Swan Sonnenschein, Lowrey and Co., London), pp. vii+152.

HEDIGER, HEINI

1934. Beitrag zur Herpetologie und Zoogeographie Neu Britanniens. Zool. Jahrb., Abt. Syst., **65**, pp. 441–582, 6 figs.

KAMPEN, P. N. VAN

1923. The Amphibia of the Indo-Australian Archipelago. (Leiden), pp. xii+304, 29 figs.

KINGHORN, J. R.

1928. Herpetology of the Solomon Islands. Rec. Australian Mus., **16**, pp. 123–178, pls. xiii–xv, 35 figs.

LESSON, R. P.

1830. "Zoologie", in M.L.I. Duperry, Voyage autour du Monde . . . sur la Corvette de sa Majesté, La Coquille, pendant les Années 1822, 1823, 1824 et 1825. (Paris), pp. iv+743, and Atlas of 157 pls.

LEVER, R. J. A. W.

1937. The Geology of the British Solomon Islands Protectorate. Geol. Mag., **74**, pp. 271–277, 1 map.

1945. The Giant Toad in the Solomon Islands. Agric. Jour. Fiji, **16**, no. 3, p. 1.

LOVERIDGE, ARTHUR

1948. New Guinean Reptiles and Amphibians in the Museum of Comparative Zoölogy and the United States National Museum. Bull. Mus. Comp. Zoöl., **101**, pp. 305–430.

MERTENS, ROBERT

1929. Zur Synonymie der Froschgattung *Batrachylodes* Boulenger. Zool. Anz., **80**, pp. 266–268.

MEYER, A. B.

1874. Über die von ihm auf Neu-Guinea und den Inseln Jobi, Mysore und Mafoor im Jahre 1873 gesammelten Amphibien. Monatsb. Akad. Wiss. Berlin, pp. 128–140.

MYERS, G. S.

1950. Ability of Amphibians to Cross Sea Barriers, with Especial Reference to Pacific Zoogeography. Proc. 7th Pacific Sci. Congress, New Zealand (in press).

NIEDEN, F.

1923. Das Tierreich. Anura I. Subordo Aglossa und Phaneroglossa; Sectio 1 Arcifera. No. **46**, pp. xxxii+584, 380 figs. (Berlin und Leipzig).

NOBLE, G. K.

1931. Biology of the Amphibia. (McGraw-Hill Book Co., New York), xiii+577 pp., 174 figs.

PARKER, H. W.

1939. Reptiles and Amphibians from Bougainville, Solomon Islands. Bull. Mus. Hist. nat. Belgique, **15**, no. 60, pp. 1–5, 1 fig.

1940. Undescribed Anatomical Structures and New Species of Reptiles and Amphibians. Ann. Mag. Nat. Hist. (11), **5**, pp. 257–274, figs. 1–3.

PETERS, W.

1877. Herpetologische Notizen, II, Bemerkungen über neue oder wenigen bekannte Amphibien. Monatsb. Akad. Wiss. Berlin, pp. 415–423, 1 pl.

SCHMIDT, K. P.

1932. Reptiles and Amphibians from the Solomon Islands. Field Mus. Nat. Hist., zool. ser., **18**, pp. 175–190.

SLEVIN, J. R.

1934. Templeton Crocker Expedition to Western Polynesian and Melanesian Islands, 1933, No. 15, Notes on the Reptiles and Amphibians, with the Description of a New Species of Sea-snake. Proc. Cal. Acad. Sci., (4), **21**, pp. 183–188.

STERNFELD, ROBERT

1921. Zur Tiergeographie Papuasiens und der pazifischen Inselwelt. Abhand. Senckenberg. Naturf. Ges., **36** (for 1920), pp. 375–436, pl. xxxi.

UNITED STATES NAVY DEPARTMENT

1944. Gazetteer (No. 1), Solomon Islands, Bismarck Archipelago and Islands off the Southeastern End of New Guinea. Hydrographic Office Pub. No. 881, pp. iv+188.

VOGT, THEODORE

1912. Beitrag zur Reptilien- und Amphibienfauna der Südseeinseln. Sitz.-Ber. Ges. Naturf. Freunde, Berlin, Jahrg. 1912, pp. 1–13.

WERNER, FRANZ

1894. Über einige Novitäten der herpetologischen Sammlung des Wiener zoolog. vergl. anatom. Instituts. Zool. Anz., **17**, pp. 155–157.

1900. Die Reptilien- und Batrachierfauna des Bismarck-Archipels. Mitt. Zool. Mus. Berlin, **1**, Heft 4, pp. 1–132, 46 figs.

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PLATES

PLATE 1

Fig. 1. *Batrachylodes vertebralis* Boulenger, pectoral girdle (ventral view)

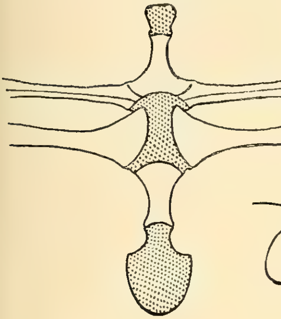
Fig. 2. *Discodeles bufoniformis* (Boulenger), pectoral girdle (ventral view)

Fig. 3. *Platymantis papuensis weberi* Schmidt, pectoral girdle (ventral view)

Fig. 4. *Platymantis solomonis* (Boulenger), pectoral girdle (ventral view)

Fig. 5. *Palmatorappia solomonis* (Sternfeld), pectoral girdle (ventral view)

Fig. 6. *Cornufer guppyi* Boulenger, pectoral girdle (ventral view)



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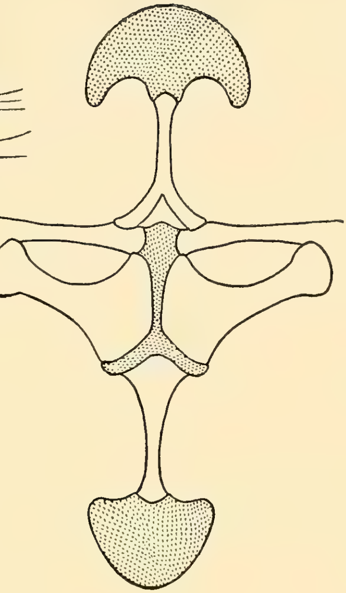

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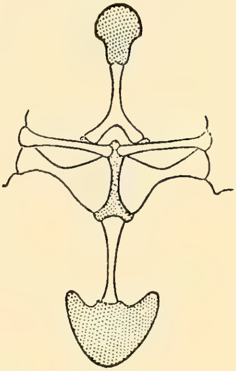

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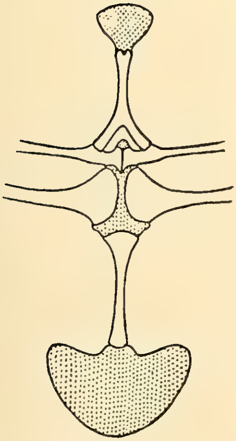

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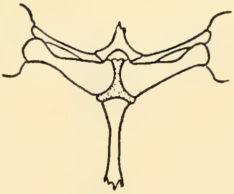

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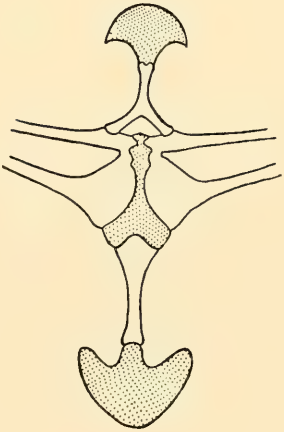
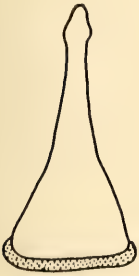


Figure 6

PLATE 2

Fig. 1. *Platymantis solomonis* (Boulenger), terminal phalanx
Fig. 2. *Batrachylodes vertebralis* Boulenger, terminal phalanx
Fig. 3. *Cornufer guppyi* Boulenger, terminal phalanx
Fig. 4. *Discodeles bufoniformis* (Boulenger), terminal phalanx
Fig. 5. *Ceratobatrachus guentheri* Boulenger, terminal phalanx



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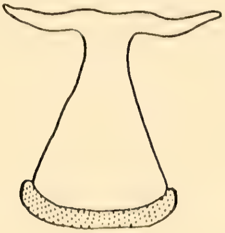

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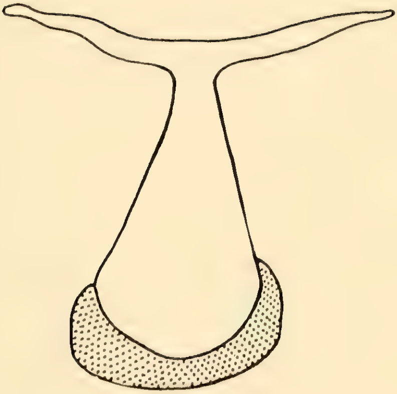

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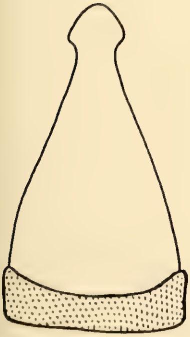

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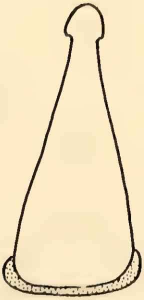
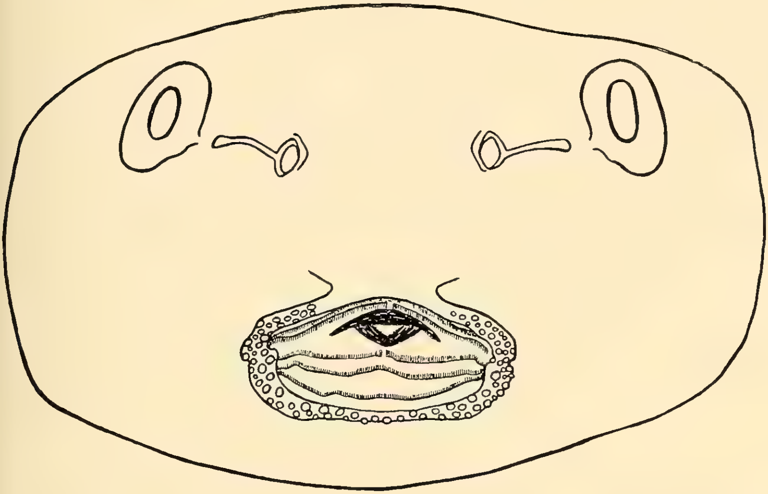


Figure 5

PLATE 3

Fig. 1. *Hyla thesaurensis* Peters, head of larva
Fig. 2. *Hyla thesaurensis* Peters, inferior view of hand



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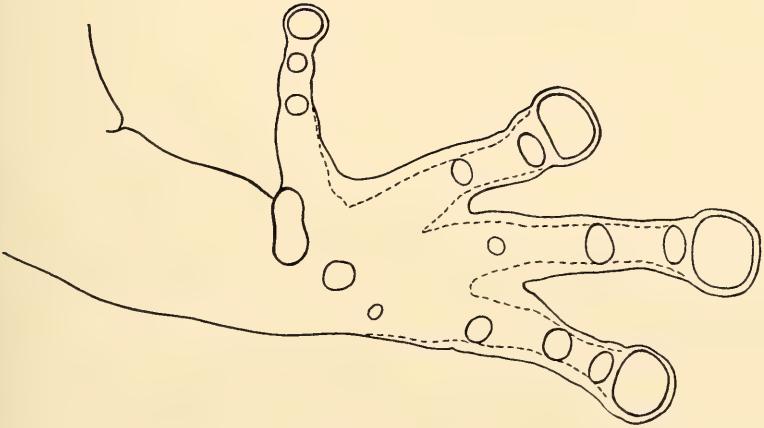
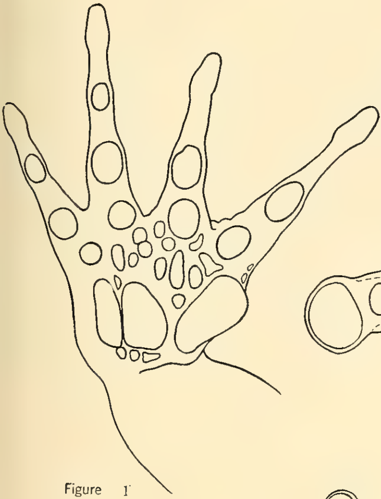


Figure 2

PLATE 4

Fig. 1. *Platymantis solomonis* (Boulenger), inferior view of hand
Fig. 2. *Hyla lutea* Boulenger, inferior view of hand
Fig. 3. *Platymantis myersi* Brown, inferior view of hand
Fig. 4. *Platymantis papuensis weberi* Schmidt, inferior view of hand



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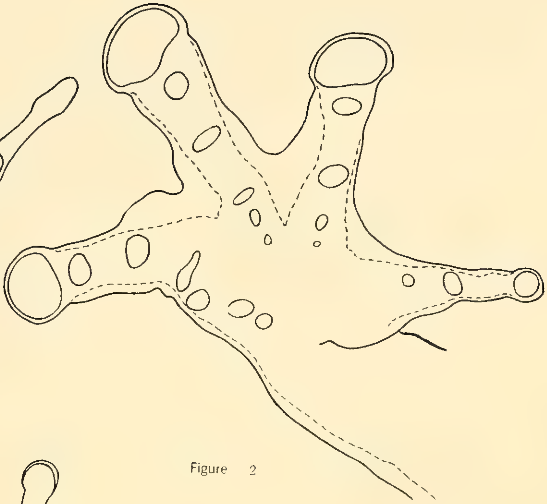

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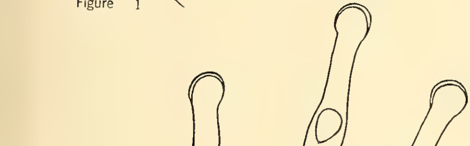

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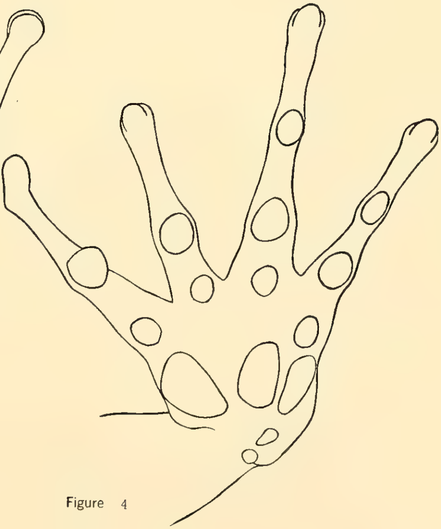
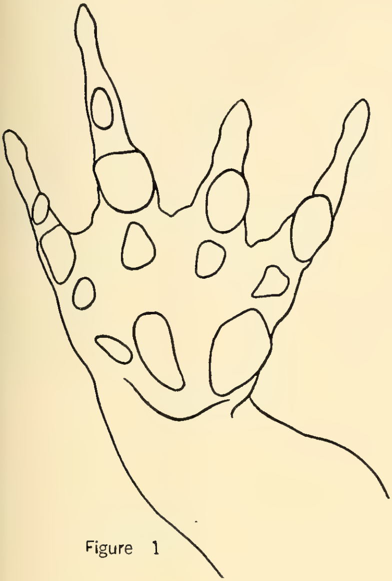


Figure 4

PLATE 5

- Fig. 1. *Platymantis aculeodactylus* Brown, inferior view of hand
- Fig. 2. *Ceratobatrachus guentheri* Boulenger, inferior view of hand
- Fig. 3. *Palmatorappia solomonis* (Sternfeld), inferior view of hand
- Fig. 4. *Cornufer guppyi* Boulenger, inferior view of hand



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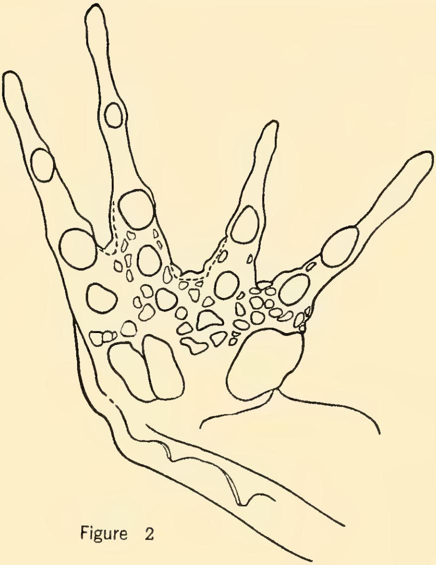

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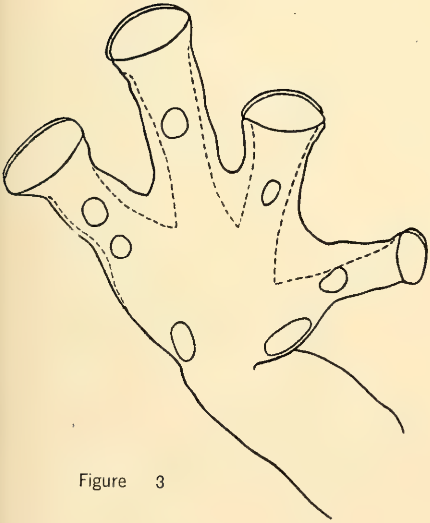

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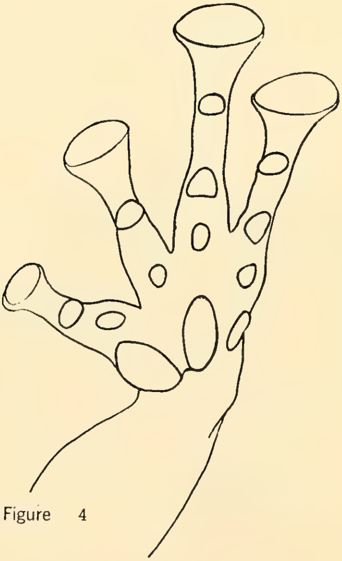
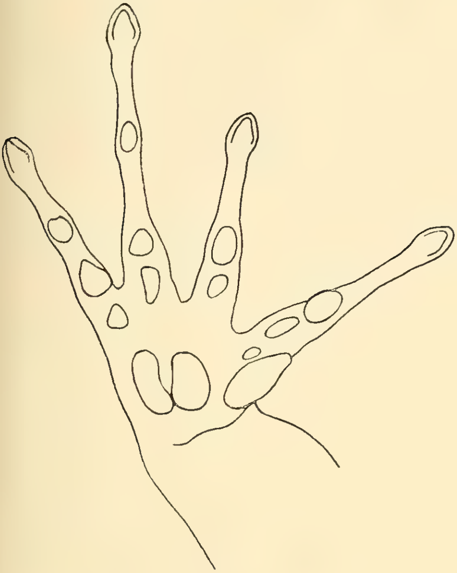


Figure 4

PLATE 6

Fig. 1. *Rana papua krefftii* Boulenger, inferior view of hand
Fig. 2. *Batrachylodes vertebralis* Boulenger, inferior view of hand
Fig. 3. *Batrachylodes trossulus* Brown and Myers, inferior view of hand
Fig. 4. *Rana papua novaebritanniae* Werner, inferior view of hand



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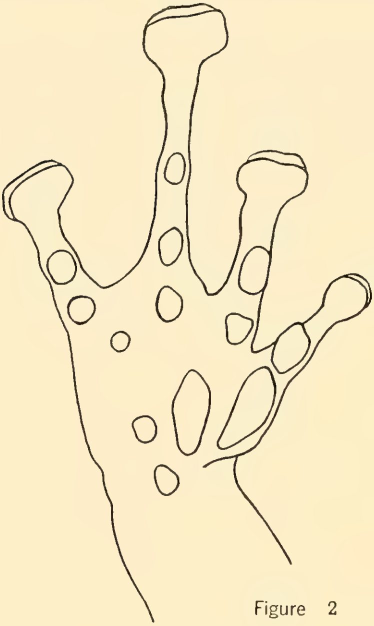

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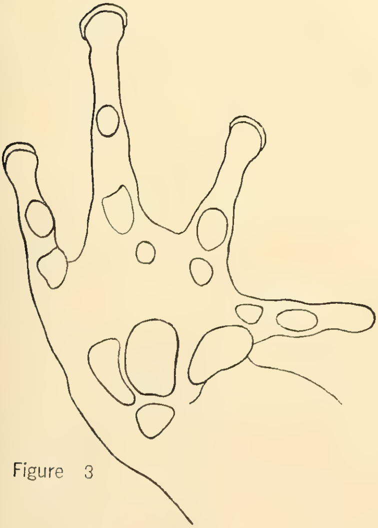

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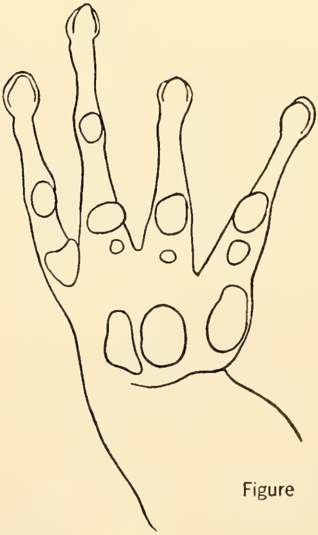
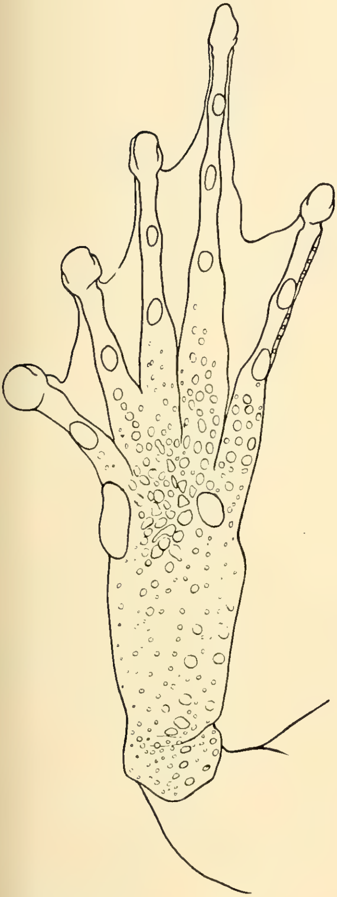


Figure 4

PLATE 7

Fig. 1. *Discodeles opisthodon* (Boulenger), ventral view of foot.
Fig. 2. *Discodeles opisthodon* (Boulenger), ventral view of hand
Fig. 3. *Discodeles bufoniformis* (Boulenger), ventral view of hand



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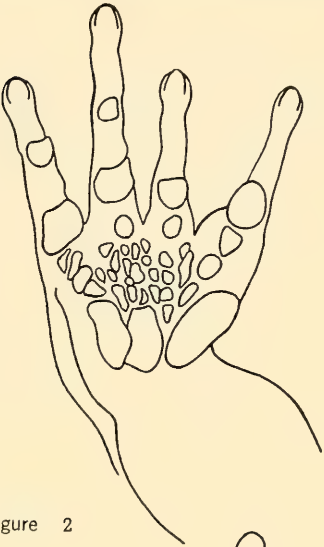

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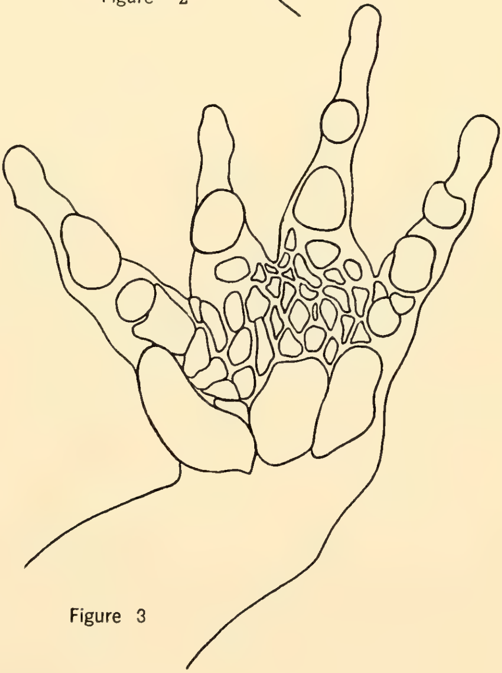
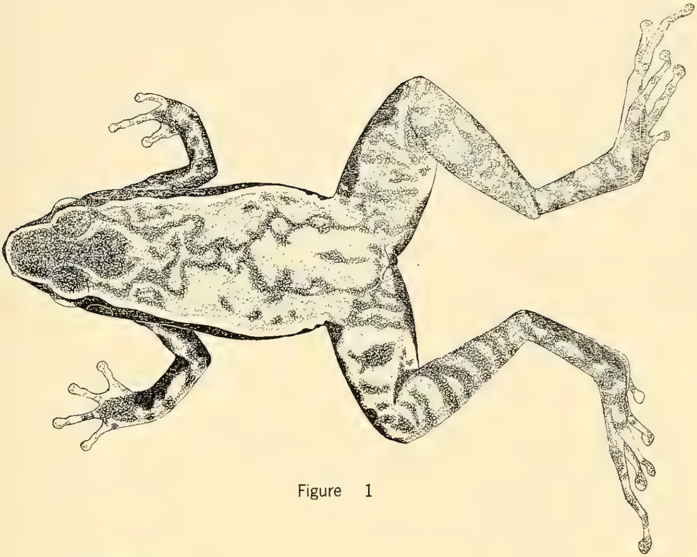


Figure 3

PLATE 8

Fig. 1. *Batrachylodes trossulus* Brown and Myers
Fig. 2. *Platymantis myersi* Brown



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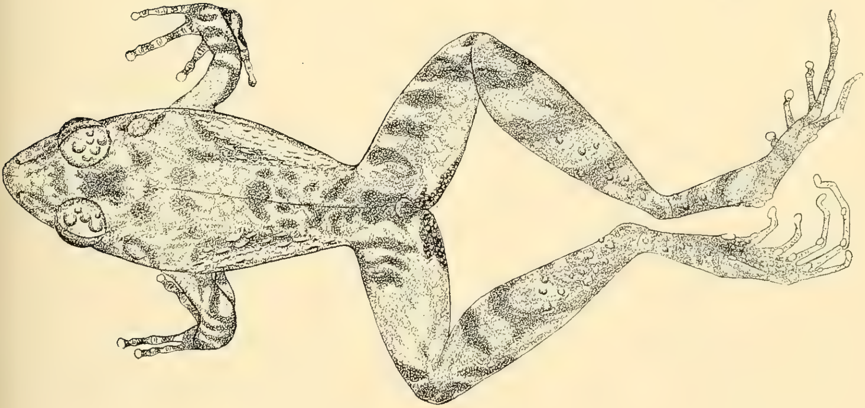

Figure 2

Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 107, No. 2

REVISION OF THE ANT GENUS SERRASTRUMA

By William L. Brown, Jr.

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
August, 1952

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No. 2.— *Revision of the Ant Genus Serrastruma*

By William L. Brown, Jr.

INTRODUCTION

When, in my division of the large and heterogeneous group which had long been known as *Strumigenys,* I demonstrated the essential differences between the "long-mandibulate" or *sensu stricto* species and the shorter-jawed forms, the latter were mostly placed in the genus *Smithistruma,* which was divided in turn into four subgenera. An African group of species which seemed distinctive was assigned the subgeneric name, then new, of *Serrastruma* (Brown, 1948, *loc. cit. infra*). At that time, the possibility still remained that previously-described but obscure short-mandibulate species might be annectant between these two groups (*Smithistruma sensu stricto* and *Serrastruma*). By 1949 (Brown, *loc. cit. infra*) all the described species but one or two were well enough known to permit the clean separation of the latter group as a genus in its own right. Subsequent investigation of strumigenite genera has amply confirmed this separation. *Serrastruma* stands as a very compact and homogeneous group, distinct from all other related genera both in the essential plan of mandibular structure and in general habitus.

The present study was initiated with the inclusion of 26 specific, subspecific and varietal names, none of which had been seriously challenged previously. This number is now reduced by synonymy to seven reasonably distinct species and two *species inquirendae.* It appears doubtful that many more new species will be recognized in this group during the strictly morphological period of investigation, and synonymy will probably still further reduce the number when certain types are made available for study.

MATERIAL STUDIED AND ACKNOWLEDGEMENTS

Specimens seen during the present investigation include types of most of the previously described forms, which I have fortunately been able to borrow or gain through exchange with various European collections. In addition, previously unstudied material in abundance has arrived from several sources. The largest single group of material is that collected during two extensive tours in Africa by Dr. Neal A. Weber of Swarthmore College and the American Museum of Natural History. Dr. Weber's material probably equals by itself the entire array of material seen by all previous authors taken together.

Future additions of material in *Serrastruma* collections will probably lead to the further reduction of the number of species rather than to proliferation. Further collection of females and males in association with workers is highly desirable, for these castes, when known, may dissolve certain doubts remaining after the present treatment. The females seem to show particular promise as a systematic aid.

I owe thanks to the following individuals and institutions for their invaluable aid in the matter of types, etc.

Dr. H. Bischoff, Zoologisches Museum der Universität, Berlin, camera lucida sketches and measurements of *reticulata* types.

Dr. Charles Ferrière, Museum d'Histoire Naturelle, Geneva, loans and sketches of Forel types.

Dr. George Arnold, National Museum of Southern Rhodesia.

M. Pierre Basilewsky, Musée du Congo Belge, Tervuren, Forel and Santschi types.

Sig. Mario Consani, Florence, Italy, Santschi and Menozzi types.

Father J. van Boven, Roermond, Netherlands, Wasmann types.

Dr. Delfa Guiglia, Museo Civico di Storia Naturale, Genoa, Emery types.

Dr. J. C. Faure, University of Pretoria.

Mr. H. St. J. K. Donisthorpe, British Museum (Natural History), Donisthorpe types.

Dr. M. R. Smith, United States National Museum.

Dr. E. S. Ross, California Academy of Sciences.

Special thanks are also due Dr. Weber and Dr. J. C. Bequaert for aid both in the matter of material and in other means essential to the success of this paper.

Other than the collections indicated above, the only important depository is the Santschi Collection in the Natural History Museum at Basle. Unfortunately, it has not been possible to view material from this latter source. Through exchange, the first important collections of *Serrastruma* have been built up in the United States at the Museum of Comparative Zoology, Harvard University, at the American Museum of Natural History, and at the U. S. National Museum. Other collections have also been augmented.

GEOGRAPHICAL DISTRIBUTION

The natural range of *Serrastruma* embraces the whole of the Ethiopian Region, except for the most arid portions. Certain species, like *lujae* and *serrula*, appear to be restricted to rain- and gallery-forest, in which they are widely distributed. *S. bequaerti* prefers the cool, humid montane forests of central parts of the continent, while *S. simoni* has an extraordinary distribution, ranging from the dry belt just south of the Sahara to the Cape region, but avoiding most rain-forest areas. We have too little data concerning the other species at present, but *lotti* and *maynei* appear to be moist-forest inhabitants, while *alluaudi* seems to range widely in several vegetational zones, but avoids or is rare in the Congo forests.

The probable youth and dominance of the genus is reflected in the collection rate, for to date more records of *Serrastruma* captures are known from Africa than for all other dacetine genera combined. *Smithistruma* is weak in species and numbers of colonies as compared to other faunas, and this is also true to a lesser extent of *Strumigenys*. The latter genus has developed a special group (group *rogeri* Emery) with high dominance, able to withstand competition from most dacetine genera, but it still seems subordinate to *Serrastruma* within its natural range. In discussing competition, it is assumed that *Serrastruma*, like related genera, feeds on collembolans captured by stalking. No confirmation of this assumption has yet come forth, but it still seems very likely to be correct in view of the basic tendency to collembolan predation in all dacetine genera so far studied.

The colonies are reported from much the same situations as are chosen by *Smithistruma* — in rotten logs, moss, under bark, under stones, in leaf litter, etc. Nest series I have studied, accompanied sometimes by collectors' remarks on their completeness, indicate that up to 300 workers and 5 queens are not uncommon colony-populations.

Outside continental Africa, flourishing populations of *Serrastruma* are known from the islands in the Gulf of Guinea and from Mauritius. One species, *ludovici*, occurs on Madagascar, but we know nothing about the abundance of the genus on this island. The Mauritius populations (*S. simoni* and *S. alluaudi*) certainly, and the Madagascar record possibly, represent recent introductions through human commerce from an African source. The possibility of "tramping" is demonstrated by the recent removal of a colony, containing males and workers at least, of *S. lujae* from plants arriving at Honolulu in U. S. Plant Quarantine. The origin of this shipment was the Belgian Congo. Probably *Serrastruma* species have been introduced elsewhere outside Africa in the tropics, but no further records have yet turned up. The tramping ability of this genus gives another hint of its dominance under varied conditions.

SERRASTRUMA Brown

Smithistruma (*Serrastruma*) Brown, 1948, Trans. Amer. Ent. Soc., **74:** 107–108.
Strumigenys of authors, *part, nec* Fred. Smith.
Strumigenys (*Cephaloxys*) of authors, *part, nec* Fred. Smith.
Strumigenys (*Trichoscapa*) of authors, *part, nec* Emery, 1869.
Serrastruma Brown, 1949, Mushi, **20:** 6, 7.

Genotype. Strumigenys simoni Emery, by designation of Brown, 1948, as subgenotype.

Gross External Morphology and Generic Characters

Worker. Resembling in size, color, sculpture and most structural features the same caste of *Smithistruma* Brown. Head together with the closed mandibles almost perfectly and rather broadly cuneiform seen in dorsal view, the sides nearly straight, evenly converging anteriorly; posterior occipital border feebly to moderately and rather broadly excised. Head seen from the side subcuneiform, rather thick posteriorly and tapering anteriorly, dorsum convex; antennal scrobes long and broad, shallow to moderately deep. Eyes small, placed just dorsad of the ventral scrobe margins posterior to the cephalic midlength, exposed to direct dorsal view.

Antennae as in other short-mandibulate strumigenite genera, with similar segmentation; scapes slender, or at most very feebly incrassate. Clypeus with a broadly triangular disc having a transverse, more or less arcuate to approximately straight "false margin" which bears the principal hairs of fringing pilosity if present. Anterior to and depressed below the level of the false margin is a translucent median lobe or apron with rounded free margin, the latter normally covering or fitting between the bases of the mandibles. This lobe has frequently been misinterpreted as an intermandibular space or other structure.

The mandibles are narrowly triangular or subtriangular, their exposed length slightly to very much longer than the clypeus; seen from the side, they are weakly arched. The armament consists of very fine serial denticulation, directly opposable throughout and occupying the entire inner (apical or masticatory) margins; at least 30 denticulations on each mandible. Most specimens show clear development of a small but stout apical and one to three minute subapical teeth, these acute, alternating with and projecting slightly beyond the even level of the denticulation as seen at high magnifications. The basalmost denticle is slightly larger and more rounded than the succeeding series, and in certain species (Group A, see below), the five or six most basal denticulae are distinctly larger, coarser and more acute than the succeeding ones and are sometimes alternate with extremely minute (intercalary) denticulae. The majority of the denticulation appears to represent secondary erosion of a very long, narrow basal lamella such as is found in *Smithistruma alberti* (Forel). If this homology is correct, it becomes apparent at once that the diminutive acute subapical teeth (alternating with lower denticles) are strictly comparable with the similarly alternating teeth of the apical series as seen in *Smithistruma* of groups *alberti* and *capitata* (Fred. Smith). In comparison with these groups of the related genus, one can find many reasons for assuming that they represent the primitive stock from which *Serrastruma* arose. I presently consider this assumption to be correct. Neither *Smithistruma* group is now found in Africa, but it appears probable that their ancestral stock once inhabited the Ethiopian Region. At any rate, the form and armature of the *Serrastruma* mandible is presently very distinctive in its modifications.

Labral lobes small and inconspicuous, but projecting and conical, much as in *Smithistruma*. The palpal segmentation (1, 1) is as in *Smithistruma*, and the maxillary palpi are similarly reduced to minute vestiges.

Alitrunk with a robust and convex promesonotum, the promesonotal suture weakly indicated or obsolete; metanotal groove strong and deeply impressed; propodeal dorsum rising from the groove and usually more or less convex, at least anteriorly. Propodeal teeth subtriangular, acute, laterally compressed, small to fairly large (obtuse and more or less vestigial in *S. bequaerti*), continued below by a narrow to cariniform infradental lamella on each side of the propodeal declivity.

Petiole with slender peduncle and distinct, raised, more or less dorsally-rounded node. Postpetiole transversely elliptical, convex dorsally, always distinctly broader than the petiolar node. Spongiform appendages vestigial to only moderately well-developed, especially on the petiole. Contrary to the observations of former authors, however, I have found *all species* to possess at least some remnants of appendages on the postpetiole. The midventral strip of the petiole is most often weak or obsolete.

Gaster as in related genera of the Strumigeniti; not markedly depressed; anterodorsal spongiform margin feeble or absent, but the usual basal costulae present, variably distinct; sting developed.

Sculpture paralleling that of *Smithistruma*. Head, mesonotum, propodeal dorsum, and usually the petiole finely and densely reticulate punctate and opaque. Gaster, except for basal costulae, smooth and shining. Pronotum and postpetiole varying in sculpture with the species, as do the sides of the alitrunk. Mandibles smooth; clypeus extremely finely punctulate-granulose, opaque, as are also the scapes and legs to a greater or lesser degree.

Pilosity basically as in *Smithistruma*. Ground hairs short, reclinate or subreclinate, fine to spatulate or spoon-shaped. Fringing hairs of scapes and false clypeal margin usually larger and more conspicuous; ground hairs of promesonotal dorsum small and usually inconspicuous. Specialized erect hairs more or less stiff, fine or narrowly spatulate, oar-shaped, or clavate, those on the nodes and gaster usually larger and heavier than those on the head; 2 to 8 on head, situated well back on occiput; mesonotum with one or two pairs, usually situated on dorsolateral tubercles; nodes and gaster with a more numerous, but still limited set each. In addition, the lateral border of each occipital lobe bears a fine, outstanding flagellate or subflagellate hair, while each humerus bears a long flagellate or spatulate hair.

Color yellow to dark ferruginous.

Female. Similar to worker, with the usual full sexual characters. In *Serrastruma*, this caste is usually larger and darker in color relative to the accompanying workers than in related strumigenite genera.

Male. Known only for a few species. Mandibles small, but opposable; triangular, the inner margins weakly produced as broadly rounded lamellae; apices acute (*S. lujae*). Otherwise paralleling the male of *Smithistruma*, especially in dark color, sculpture, etc.

Specific Characters, Variability, etc.

Serrastruma betrays its relative youth as a genus and differs from most other dacetine genera in the decided variability of some of its species and in the concomitant slightness of specific distinctions. Because of these qualities, it is a "difficult" genus from the taxonomist's point of view. Most of the past taxonomic confusion in the group, however, cannot be blamed entirely upon variation or slightness of specific distinctions. This confusion was due partly to the fact that *Strumigenys*, in the old, portmanteau sense, has effectively concealed, one might say "swallowed up", the group, so that efforts to distinguish the species have been dissipated in comparison with a much larger number of short-mandibulate forms actually having only a distant relationship to *Serrastruma*. Thus, the two species *ludovici* Forel and *reticulata* Stitz were effectively lost into *Strumigenys sensu stricto* when subsequent classifiers interpreted too literally the uncannily misleading original descriptions. Camera lucida drawings of types enable me to place these two forms quite certainly in *Serrastruma*.

Beyond this, the extensive synonymy must be laid to pure carelessness in construction and subsequent interpretation of descriptions. Apparently, when authors were describing a "new" form, reference was had almost entirely to previous descriptions instead of to types or reliably identified material, even though the latter might be readily available, or even in the specialist's own collection. That many of the older descriptions were seriously in error is now clear. The lack of critical appraisal of descriptions in the past is amazingly general, as one can determine from reference to the discussion of the synonymy of *S. simoni* Emery, below. Unfortunately, the poor systematic work visted upon *Serrastruma* has also been widespread among other, much larger formicid groups that will not be so easy to untangle. A conclusion to be drawn from *Serrastruma* is that, though a given group of ant species may show variation and blurring of interspecific characters, these "difficult" qualities are seldom of the degree of seriousness indicated by the usually excessive number of synonyms and infraspecific variants named in the group. Thus, in the case of *S. simoni*, Santschi repeatedly described forms the types of which, under present direct comparison, fail utterly to show the differences cited in the original descriptions.

In my own attempt to sort *Serrastruma* material into species, a very careful search of the worker caste was made in an attempt to recognize features of consistent value in separating species. Few were found, and this fact is reflected in the very large new synonymy. However, one seemingly constant and most useful character concerns the mandibular dentition, falling into two sorts as follows:

Group A

In *alluaudi, lotti* and *ludovici*, the mandibles are long (MI 40 or more), relatively slender and evenly tapered toward their apices; basal quarter or fifth of the apical margins each with the denticulae suddenly and decidedly larger, coarser, more irregular and more acute than those following distally. This coarse basal series usually numbers 5–6 units on each mandible; each unit may alternate with an indefinite minute denticle.

Group B

In *lujae, serrula, maynei, bequaerti* and *simoni* the mandibles are a bit more robust and are usually under MI 40, rarely slightly more. The apices are somewhat more blunted in dorsal view. The denticulation is fine (*lujae, maynei, bequaerti*) or extremely fine (*serrula, simoni*), and the denticulation toward the base of the apical border is not or only very slightly and *gradually* coarsened, regular and not acute; the basalmost denticle may, however, be slightly enlarged and sublamelliform.

In doubtful cases, the denticulation is best examined by placing the mandibles in dark contrast over a brightly lighted white background. The differences are so plainly apparent that, if magnification is at the necessary 60–80 diameters, contrast lighting should rarely be necessary.

Other characters of use in distinguishing species concern the sculpture, especially of the pronotum and nodes of the pedicel; relative head width; pilosity; development of propodeal teeth and lamellar or spongiform appendages, etc. Measurements and proportions given are considered the bare minimum essentials, here cited for the first time. Former statements of "total length" have been highly inaccurate and are not at all comparable, even in the consecutive descriptions of one author.

Abbreviations:

HL — Maximum measurable length of head from dorsal view, mandibles excluded. Measurement is made from the center of the *true* anterior clypeal margin to a line connecting the posterior occipital extremities.

CI — Cephalic index: maximum measurable width of head expressed as a percentage of the head length, or head width/HL × 100.

MI — Mandibulo-cephalic index: "exposed length" of mandibles expressed as a percentage of the head length. Measurement is made in the fully closed condition from the center of the true anterior clypeal margin to the extreme apex of the most advanced mandible. Exposed mandibular length/HL × 100.

These measurements and proportions are standard in my works on the Dacetini.

SYSTEMATIC TREATMENT BY SPECIES

In the synonymies below, only essential references are cited, and those appearing subsequent to about 1920. Full synonymies are cited in:

Emery, C., 1922, in Wytsman's Genera Insectorum, Fasc. 174, pp. 320, 324 (as *Strumigenys*).

Wheeler, W. M., 1922, Bull. Amer. Mus. Nat. Hist., **45:** 918–920, 1034 (as *Strumigenys*).

An early key to African *Strumigenys* is of interest only as an illustration of the early confusion of the taxonomy of the group:

Santschi, 1913, Bull. Soc. Ent. France, pp. 257–259.

The best habitus figures of *Serrastruma* (though portraying the mandibular dentition as a somewhat inaccurate convention) are those of Eidmann, for which references are given in the synonymy of *S. lujae*, below.

Cited with the descriptions below are all type localities, whether or not types have been examined. All other records represent specimens actually seen during the course of this work.

SERRASTRUMA ALLUAUDI (Santschi) new combination

Strumigenys (*Trichoscapa*) *alluaudi* Santschi, 1910, Ann. Soc. Ent. France, **79**: 360, worker, female; original description.

Strumigenys rothkirchi Wasmann, 1918, Ent. Mitt., Berlin, **7**: 142, Pl. 2, figs. 9, 10, worker. NEW SYNONYMY.

Strumigenys (*Cephaloxys*) *raymondi* Donisthorpe, 1945, Ann. Mag. Nat. Hist., (11) **12**: 779, part., worker. 1946, *Ibid.*, **13**: 32; part. NEW SYNONYMY.

Worker. HL 0.55–0.60 mm., CI 75–78, MI 40–44. Mandibles of Group A form. Postpetiole swollen and very convex, its surface weakly to distinctly sculptured, more or less opaque. Sides of alitrunk with at least some punctulate-reticulate sculpture; not completely smooth and shining as in *simoni*, and the propodeal teeth slightly less well-developed than in *simoni*. Otherwise, this species is very much like *simoni* and likely to be confused with that species (*q. v.*).

Pilosity variable, especially the shorter ground hairs. At least part of the variation, both in erect and ground pilosity, seems to be due to differing amounts of adherent foreign matter, possibly a hardened secretion, which makes the hairs appear thicker at their apices when abundant. Color variable as in *simoni;* vertex often infuscated.

I have not seen types of *alluaudi*, but specimens determined by Dr. Arnold and stemming from Natal are considered near-typical or typical. Dr. Arnold was in close contact with Santschi for many years, and his specimens agree closely with Santschi's characterization. A *rothkirchi* type from the Wasmann Collection, kindly sent by Father van Boven, agrees closely with the Natal specimens and with a cotype of *raymondi* sent by Mr. Donisthorpe. Mr. Donisthorpe has disagreed (*in litt.*) with my synonymy of *raymondi*, and a subsequent visit to the British Museum may possibly explain his disagreement. The specimen labelled "type" in the British Museum is actually a specimen referable to *simoni*, while those labelled "cotypes" (= paratypes in American usage) are divided between *simoni* and *alluaudi* specimens. Evidently both species are well established on Mauritius, and Mr. Donisthorpe has confused them under a new name. Specimens taken by Weber at Kampala, Uganda are the most atypical I have seen, but even here the difference is largely one of pilosity and is not considered taxonomically significant.

S. alluaudi is widely spread in Africa, and seems to have been carried about a greal deal by human commerce. The "*rothkirchi*" specimens from Mt. Kamerun may, as Dr. Bequaert has suggested, have been taken in or near the former German horticultural experiment station. During the period of German administration, plants were brought here from all parts of Africa, and might easily have harbored migrant *Serrastruma*. Otherwise, *alluaudi* seems to have its main natural range in eastern Africa. The Mauritius records must be put to tramp migration, while the Madagascan *ludovici*, quite possibly identical with *alluaudi*, may have come from Africa in the same way. *Alluaudi* has not yet been taken in the Congo rain-forests, and in this respect it resembles distributionally the related *simoni*. However, further investigation may show that *lotti*, a smaller but similar species which ranges into the eastern Congo Basin, is only an extreme variant of *alluaudi*.

The male and female of *alluaudi* have not been studied by me.

Type locality. Grotto of Tanga, "Kulumuzi," German East Africa (C. Alluaud). Types are probably in the Paris Museum and the Santschi Collection.

Localities for material examined. Kampala, Uganda (N. A. Weber, series no. 1503). Eshowe, Natal (G. Arnold). Soppo, 730 m., Kamerunberg (von Rothkirch); cotype of *rothkirchi*. Cocotte Mt., Mauritius (R. Mamet); cotype of *raymondi*. Other *raymondi* cotypes from Mauritius briefly examined in the British Museum, several series.

SERRASTRUMA LOTTI (Weber) new combination

Strumigenys (*Cephaloxys*) *escherichi* subsp. *lotti* Weber, 1943, Bull. Mus. Comp. Zool. Harvard, **93**: 327, 378–379, Pl. 15, fig. 13, worker, female, biology; original description.

Worker. HL 0.46–0.49 mm., CI 80–84, MI 42–46. *Female* considerably larger than the worker and darker in color, but not large enough to fit readily as the female of *alluaudi*, considering the workers of the latter species. Cotypes have been compared directly with additional specimens from the localities cited below, and agreement is close. This form is essentially a smaller and lighter-colored version of *alluaudi* with finer pilosity. The form and denticulation of the mandibles in the two species are quite similar, although those of *lotti* seem slightly longer relatively. The sculpture of the pronotum is similar and equally variable in both species. Future collections may show that intergrades occur and that synonymy is indicated, but the present material does not support this. The species *calypso* (*species inquirendae* section below) is poorly described, and may quite possibly be the same as *lotti*, over which it has nomenclatorial precedence.

Errors in Weber's description should be noted. *S. lotti* is not attachable to "*escherichi*" because of the dentitional differences. The figure shows the shape of the scape quite wrongly, and depicts the funiculus as seven-segmented, whereas the funiculus, as in all *Serrastruma*, is really five-segmented.

This species has been taken in the eastern Congo and in the adjacent gallery-forests of the Sudan; it is probably widespread in eastern Africa.

Type locality. Lotti Forest, west slope of Imatong Mts., Anglo-Egyptian Sudan (N. A. Weber, series no. 1451). Cotypes are in Dr. Weber's collection and in the Museum of Comparative Zoology, Harvard University, as well as in other institutions. Several workers and a dealate female have been examined from the type series.

Material examined from other localities. Belgian Congo: Stanleyville (A. Collart). Beni to Irumu (N. A. Weber, no. 2124). Anglo-Egyptian Sudan: Kagelu, Equatoria (Weber, no. 1284).

SERRASTRUMA MAYNEI (Forel) new combination

Strumigenys maynei Forel, 1916, Rev. Suisse Zool., **24:** 427, worker, female, male; original description.

Strumigenys maynei var. *latiuscula* Forel, 1916, *Ibid.*, p. 428, worker. NEW SYNONYMY.

Worker. HL 0.52–0.56 mm., CI 83–87, MI 36–40. Color yellowish- to medium ferruginous. Mandibular dentition of Group B, and closely resembling that of *lujae*. Readily distinguished by means of the sharp, definite, fine and close longitudinal costulation (or striation) of the pronotum, by the broad head, with pronounced, thin lamelliform borders along the upper margins of the antennal scrobes, and by the small but conspicuous, broadly spoon-shaped hairs of the cephalic and promesonotal ground pilosity. The differences in head width and color between the types of *maynei* and its variety *latiuscula* presently before me are perceptible, but scarcely significant for taxonomic purposes. The very much greater variation shown by different series of the related *lujae* confirms for me the opinion that *latiuscula* should never have originally received nomenclatorial distinction.

Type locality. Stanleyville, Belgian Congo (Kohl); three cotypes examined from the Forel Collection, one of which has been retained as an exchange in the Museum of Comparative Zoology.

A single cotype worker of var. *latiuscula* has been received in exchange from the Musée du Congo Belge; the type locality for this form is Eala, Belgian Congo (R. Mayné). No other material has been seen.

SERRASTRUMA LUJAE (Forel) new combination

Strumigenys lujae Forel, 1902, in Wasmann, Allg. Zeitschr. Ent., **7:** 51, nota, Pl. 1, fig. 1, worker; original description.

Strumigenys reticulata Stitz, 1910, Mitt. Zool. Mus. Berlin, **5:** 141, worker. NEW SYNONYMY.

Strumigenys (*Cephaloxys*) *glanduscula* Santschi ("new var."), 1919, Rev. Zool. Afr., **7:** 88, worker. Bequaert, 1925, *Ibid.*, **8:** 146, biology. NEW SYNONYMY.

Strumigenys (*Cephaloxys*) *gerardi* Santschi, 1923, Rev. Zool. Afr., **11:** 287–288, worker. NEW SYNONYMY.

Strumigenys (*Cephaloxys*) *aequalis* Menozzi, 1942, Zool. Anz., **140:** 177–178, worker, female; original description. Eidmann, 1943, Mitt. H. Göring Akad. Deutsch. Forstwiss., **1:** 262, fig. 25, worker, biology; 1944, Zool. Jahrb. Syst., **76:** 457–458, figs. 15, 16, worker, biology. NEW SYNONYMY.

Worker. HL 0.52–0.71 mm., CI 77–83, MI 37–42. Distinguished from all other species except *serrula* and *bequaerti* (*q. v.*) by virtue of its Group B mandibles, evenly rounded, densely reticulo-punctulate pronotum, its fine erect and ground pilosity of the head, and its spongiform appendages, which are strongly reduced, especially the mid-ventral petiolar strip; the latter appears as a low, blunt, non-spongiform, carina-like vestige. Funicular segments II and III varying from slightly to considerably longer than thick. Postpetiole with weak appendages; dorsal surface usually reticulate-punctulate and opaque, but occasionally having the sculpture effaced and the surface nearly completely smooth, shining. Median carinula of the pronotum absent or feeble. Color somewhat variable, but usually lighter or darker yellowish-ferruginous.

Female larger than workers from the same nest, and usually a bit darker. Lateral occipital hairs borne on very low, weakly convex lamellae or carinae which do not occur, or at least are not readily apparent, in the workers.

The *males* vary in sculptural and other details, even within one nest series. The color is variable, but usually is predominantly dark castaneous or brownish-black, with the alitrunk lighter. The volsellae-laciniae are not markedly different from those of many *Smithistruma* species; these will be figured in another paper.

The extensive synonymy proposed here for *lujae*, unlike that of *simoni*, is at least partly a reflection of the considerable variation shown by different nest series. Forel originally described the petiole and postpetiole as without spongiform appendages, although a type received from the Wasmann Collection shows a fine posterodorsal collar on the petiole and small but distinct ventral postpetiolar appendages of spongiform consistency. This misdescription threw later authors off the track rather badly, as Santschi's hesitant description of *glanduscula* clearly shows. A cotype of *glanduscula* in the Museum of Comparative Zoology (on loan from the Musée du Congo Belge) compares well with the *lujae* cotype, but is slightly smaller.

Stitz described *reticulata* so poorly that all subsequent workers were led to include it among the species of *Strumigenys sensu stricto*. A camera lucida sketch and measurements of a type, kindly furnished by Dr. Bischoff, show that this species is only a small variant of *lujae* like those taken in the Honolulu Plant Quarantine.

Beyond rectification of these obvious errors, the treatment of *lujae* becomes more subject to theoretical considerations. The series I have actually seen represent 17 separate nests from nearly as many localities. While each nest series is relatively homogeneous in size and proportions, certain of the series appear very different, especially in size, when directly compared. The various series may be arranged into a completely intergradient row, each broadly overlapping the next in all variable characters, and connecting the extremes. Such slight differences as occur in proportions, mandibular denticulation, pilosity, development of propodeal teeth and pronotal carinula, etc. seem to be correlated with overall size, and one cannot escape the impression that the very noticeable size difference, would, if known only from the inspection of a few series, form the most striking means of distinguishing taxonomic entities. Nevertheless, the intergradation is solidly established in the present material, and this alone will serve to negate any separation in the absence of evidence for geographical apportionment.

Large specimens convene well with a type of *gerardi*, medium ones with types of *lujae* and *glanduscula*, and the smallest ones with *reticulata* and the specimens from Hawaiian Plant Quarantine. The largest specimens I have seen (Saõ Tomé) are larger than the *gerardi* types, while the smallest (Burunga and Honolulu) are smaller than cotypes of *aequalis* examined through the courtesy of Signor Consani. The essential relationship (and non-distinctness) of all these series seems to me more striking than the known variable "specific characters," and I have emphasized the former quality in the synonymy. The variability is such that future investigation may well show that *serrula* and even *bequaerti* are to be included.

S. lujae is clearly a sylvicolous species, and the most commonly-collected form of *Serrastruma* in the equatorial forest belt and adjacent gallery-forests. Its presence on the islands in the Gulf of Guinea and in plant shipments at Honolulu indicates with what ease it can spread to new areas. The nests are made in rotten wood or in the soil or soil cover. I have examined series from nests containing up to 300 workers and four or five queens plus numerous winged forms of both sexes, males predominating. Males are often present as fully-pigmented free imagoes while the majority of the females are still in the pupal stage. Large nests are often infested with an apparent myrmecophile- a small ferruginous staphylinid beetle.

Type locality. Morumballe, on the Zambesi River, Portuguese East Africa (E. Luja). Types are in the Forel and Wasmann Collections; I have seen one worker from the latter source.

Additional localities for material seen. Belgian Congo: South of Watsa, Ituri Forest. West side of Ruwenzori (N. A. Weber, nos. 2139, 2112). Burunga (J. C. Bequaert). Yambuya (J. C. Bequaert); cotype of *glanduscula.* Manyema (Gerard); cotypes of *gerardi.* Precise source unknown, via U. S. Plant Quarantine, Honolulu, Hawaii; workers and males, in plants. Cameroon: Gross Batanga (G. Schwab). Saõ Tomé Island: Makambrera, 4000 feet. Roca Zampalma, 2500 feet (B. Malkin); three colonies and a stray worker. Fernando Po Island: Concepcion (H. Eidmann); cotypes of *aequalis.* Uganda: Fort Portal (N. A. Weber, nos. 2095, 2102, 2103); several collections, including females.

SERRASTRUMA BEQUAERTI (Santschi) new combination

Strumigenys (*Xephaloxys*) [*sic*] *bequaerti* Santschi, 1923, Rev. Zool. Afr., **11:** 286–287, worker; original description.

Strumigenys (*Cephaloxys*) *bequaerti* Bequaert, 1925, Rev. Zool. Afr., **13:** 146, biology.

Worker. HL 0.58–0.61 mm., CI 73–78, MI 35–37. Quite similar to medium-sized specimens of *lujae,* but with the head narrower on the average. Second and third funicular segments long and cylindrical, nearly or quite twice as long as thick.The chief distinction of *bequaerti* lies with its vestigial propodeal teeth; these are extremely reduced, little more than pronounced angles, obtuse or subrectangular in profile. Other characters as in *lujae.*

This form may eventually prove to be a montane subspecies or even a synonym of *lujae.* Dr. Bequaert says (*loc. cit.*) of the type collection (in translation):

"The nest of this ant was found at about 2200 meters altitude in the humid montane forest of the Butagu Valley, on the west side of Ruwenzori. It was situated in the humid and strongly shaded soil."

Additional specimens, which convene well with the cotypes at my disposal, were taken by F. Meneghetti in the similar cool montane forest (Mau Forest) of the Kenya Colony. This series, which contains winged females, reached me through the courtesy of Signor Consani, who has indicated his desire to prepare the description of this winged caste.

Cotypes are in the Musée du Congo Belge, Museum of Comparative Zoology, Consani Collection, and presumably in the Santschi Collection.

SERRASTRUMA SERRULA (Santschi) new combination

Strumigenys lujae var. *serrula* Santschi, 1909, Ann. Soc. Ent. France, **78**: 390–391, worker; original description.

Strumigenys (*Cephaloxys*) *serrula* Santschi, 1923, Rev. Zool. Afr., **12**: 288, fig. 4c, worker.

Strumigenys (*Trichoscapa*) *concolor* Santschi, 1914, Boll. Lab. Zool. Portici, **8**: 375, worker. NEW SYNONYMY.

Strumigenys (*Cephaloxys*) *uelensis* Santschi, 1923, Rev. Zool. Afr., **12**: 289–290, fig. 4b, worker. NEW SYNONYMY.

Worker. HL 0.45–0.52 mm., CI 80–89, MI 34–39. The distinctions between the worker of this species and that of small *lujae* series is not very satisfactory. The smaller size, shorter mandibles, and usually broader head will serve to distinguish most *serrula* specimens. Even the smallest *lujae* specimens will not show these dimensions and proportions all within the *serrula* range and simultaneously. Many *serrula* specimens from French Equatorial Africa and from West Africa (*concolor* cotype) show a well-developed lamelliform margin along the dorsal scrobal borders. On each side at the point of greatest lateral expansion of the occipital borders, these margins end rather suddenly at a gentle depression, from which arises the lateral flagelliform hair. Specimens from the Belgian Congo and Uganda often lack the lateral occipital depression or show it in very weak form, while others from these localities have it distinctly developed. Females from all localities seen so far all have the depressions distinctly developed. This character will serve to distinguish the females and most workers of *serrula* from *lujae*, in which the female, it will be remembered, has the lateral occipital hair arising from a low, convex ridge. Both female castes of *serrula* seen in full-face view tend to have the external mandibular margins very feebly convex to straight; in *lujae* the same margins are straight to feebly concave. A *serrula* female from south of Watsa in the Belgian Congo (Weber, no. 2139) shows a total (synthetic aggregate) length, mandibles included, 2.47 mm., HL 0.52 mm., CI 87, MI 35. Other females from various localities showed scant variation away from these values. The difference in size from the *lujae* female is considerable.

In sculpture, the worker is like that of *lujae,* but some specimens have the punctulation of the pronotum overlain with feebly-suggested longitudinal striation or costulation. The hairs of the ground pilosity are usually slightly broader than those of *lujae,* and the punctulation of the upper occipital region appears relatively coarser. The node of the petiole is not so high or so steep anteriorly as in *lujae.* The denticulation of the mandibles appears to be finer than in small *lujae* specimens, and a magnification of 80–100 diameters is needed to resolve the separate units with any clarity. Color varying from pale yellow to medium ferruginous. In spite of all the characters cited, the species remains doubtfully distinct from *lujae.* In the series collected by Dr. Weber, specimens of *lujae* and *serrula* were on at least three occasions (nos. 2095, 2103 and 2139) presumably taken together or in close proximity. Dr. Weber's field notes, not presently available, will be of considerable interest when published. Were it not for the seemingly clearcut differences in the female caste, I should be tempted to combine the small and large forms under the name *lujae.*

A *concolor* type sent by Sig. Consani, mentioned above, seems to fall within the limits of (continuous) variation of the abundant series here referred to *serrula,* and nothing in Santschi's descriptions will serve to force separation of the two. The form *uelensis* is separated on the basis of the supposedly straight anterior clypeal margin. I have seen no specimens from the type series, but review of Santschi's description and figure convinces me that he overlooked the anterior clypeal lobe or apron; his anterior border is actually the false border. Santschi was unsure of the distinctness of this form himself, and it seems certain that we owe the name to his hasty examination of the types.

Type locality. Brazzaville, Congo (Weiss). Type not seen.

Additional material seen. Abundant material collected by Dr. Weber at virtually all of the localities in the Belgian Congo and Uganda from which he also secured *S. lujae,* also a series collected by him at Haut Mbomu in French Equatorial Africa. A cotype of *concolor* Santschi: type locality, Aburi, Gold Coast (Silvestri).

SERRASTRUMA SIMONI (Emery) new combination

Strumigenys simoni Emery, 1895, Ann. Soc. Ent. France, **63**: 42, Pl. 2, fig. 21, worker; original description.

Strumigenys escherichi Forel, 1910, Zool. Jahrb. Syst., **29**: 261, worker. NEW SYNONYMY.

Strumigenys cognata Santschi, 1910, Ann. Soc. Ent. France, **79**: 362, worker. NEW SYNONYMY.

Strumigenys (*Trichoscapa*) *cognata* st. *boerorum* Santschi, 1913, Bull. Soc. Ent. France, p. 259, worker. NEW SYNONYMY.

Strumigenys (*Trichoscapa*) *biconvexa* Santschi, 1913, Bull. Soc. Ent. France, p. 258, worker. NEW SYNONYMY.

Strumigenys escherichi subsp. *limbata* Forel, 1913, Deutsche Ent. Zeitschr., p. 222, worker. NEW SYNONYMY.

Strumigenys escherichi var. *cliens* Forel, 1913, Rev. Zool. Afr., **2**: 317, worker. NEW SYNONYMY.

Strumigenys (*Trichoscapa*) *escherichi* subsp. *cognata* var. *obscuriventris* Santschi, 1914, Boll. Lab. Zool. Portici, **8**: 375, worker. Preoccupied name, *nec* Wheeler 1908.

Strumigenys (*Trichoscapa*) *escherichi* subsp. *cognata* var. *fusciventris* Santschi, 1915, Ann. Soc. Ent. France, **84**: 261; *nom. pro obscuriventris.* NEW SYNONYMY.

Strumigenys (*Trichoscapa*) *alluaudi* subsp. *nigeriensis* Santschi, 1914, Boll. Lab. Zool. Portici, **8**: 376, worker. NEW SYNONYMY.

Strumigenys (*Cephaloxys*) *raymondi* Donisthorpe, part. (see *alluaudi*).

Worker. HL 0.52–0.60 mm., CI 75–83, MI 35–42. Mandibular denticulation of Group B, extremely fine and regular, the basal denticles not or virtually imperceptibly enlarged. Dr. Arnold has pointed out (*in litt.*) that the posterolateral mesonotal angles are better developed than in *alluaudi* and that the postpetiole is much less strongly convex and smaller. Otherwise, except for the striking dentitional difference and the completely smooth and shining sides of the alitrunk in *simoni*, the two species are very similar (see *alluaudi*, above). In *simoni*, as in *alluaudi*, the pronotum is more or less shining, with a median carinula and weak, well-spaced oblique costulation on each side of the dorsum. The dorsal surface of the petiole is punctulate, but that of the postpetiole is completely smooth and shining *when clean.*

Spongiform appendages rather well-developed on the petiole, including the midventral strip, and on the postpetiole. The propodeal teeth are the largest in the genus, and like those of the other species, are sharply upturned. The *female* is conspicuously larger and darker than the worker, but otherwise similar. Male not seen.

S. simoni is very widely distributed south of the Sahara. It ranges from Makapan in the Transvaal and Angola to Eritrea and French Guinea. Dr. Bequaert, who is quite familiar with African vegetation, has checked the localities for this ant very carefully with me. From the data, it appears that *simoni* avoids the regions of true rain- and gallery-forest quite consistently, although crossing the political boundaries of the Belgian Congo at several places. This form is at home in the more open forest and savannah covering such a large part of the continent. Colonies are found in rotten wood, under stones, and in the soil cover. This is perhaps the most familiar, and certainly the most-named, species of *Serrastruma.*

The extensive synonymy is truly surprising, for this species shows little variation compared to *lujae*, *serrula* or *alluaudi*, even though its range is wider. The confusion began with Emery's original description, which states unequivocally that the basal gastric costulae are lacking. Later authors all utilized this as a difference when describing forms which were obviously close. In reply to my specific request, Dr. Delfa Guiglia has kindly examined the type material in the Emery Collection. She states that the gastric dorsum is basally costulate, and her accompanying sketch shows quite clearly the costulation, which differs in no way from that of the forms next considered. With due allowances for Emery's draughtsmanship, which often erred in small details, the original characterization fits, and fits only the specimens before me.

I have examined type specimens of all the species mentioned in the synonymy except *biconvexa*, *boerorum* and *limbata*. Of the last two species, I have seen specimens, presumably authentic because determined by Dr. Arnold and collected at or near the type localities. The *limbata* specimen may be from the original series. Dr. Arnold states *in litt.* that he has been able to find no differences between *limbata* and *boerorum*, and he has had material from Forel and Santschi.

My material is outstanding in its uniformity, and cannot be distinguished from *simoni* by any satisfactory character. The descriptions of Forel and Santschi frequently differ in important details from the corresponding types, and one cannot but wonder at the thoroughness of observation leading to such publication. In 1910 and 1913 Forel and Santschi crossed in description, but neither attempted an investigation they must have known could scarcely have avoided unearthing synonymy; the result was some minor juggling of subspecific names and further confusion. In each case, both authors apparently compared their specimens against the previous descriptions, and not against authentic specimens. But the descriptions, which they themselves had so largely written, misled them still further. Santschi's description of the homonym-synonym *obscuriventris* on the same page with the synonym *nigeriensis* remains inexplicable, especially since the types of the forms are as alike as two ants can be. These were collected by Silvestri at the same Nigerian locality (types sent by Sig. Consani).

In lieu of a continued detailed statement of the reasons for the new synonymy, I can only point to the lack of reliable differences among the types seen by me, and which have been directly and painstakingly compared in all directions. The species *biconvexa* Santschi, of which I have seen no authentic material, appears to be based on small, dark specimens of *simoni*. If differences other than these questionable ones occur in the types, Santschi has not mentioned them in his publications or proved them by his figures. In the types of the synonyms and the abundant additional material I have seen, the chief variation, and that slight, is in relative length of the mandibles and in depth of color; no significant geographical apportionment of these characters can be detected. The coloration ranges from medium to deep ferruginous.

Type locality. Makapan, Transvaal (Simon).

Localities for other material examined. Southern Rhodesia: Victoria Falls. Bulawayo (G. Arnold). Zululand: Sordwana. Richards Bay; specimens from 3 colonies, including females (J. C. Faure). Belgian Congo: Elisabethville (J. C. Bequaert); 4 cotypes of var. *cliens.* Stanleyville (Kohl). Nigeria: Olokomeji (F. Silvestri); specimens from type series of *nigeriensis* and *obscuriventris ex* Consani Collection. Angola: Cucala, Benguela (J. Cruchet); cotype, Musée du Congo Belge, of *cognata.* Eritrea: Ghinda (K. Escherich); cotypes of *escherichi,* Forel Collection and American Museum of Natural History. French Guinea: Kindia (F. Silvestri); det. *cognata* by Santschi. Mauritius: Several series (*raymondi* types in part.), British Museum.

SPECIES INQUIRENDAE

SERRASTRUMA LUDOVICI (Forel) new combination

Strumigenys ludovici Forel, 1904, Ann. Mus. Acad. Sci. S. Petersbourg, **8:** 369, worker, original description.

This species has been considered by all previous authors to belong to *Strumigenys sensu stricto.* A camera lucida sketch graciously prepared for me by Dr. Ferrière from the type (presently designated *lectotype*) in the Forel Collection shows conclusively that *ludovici* is a member of the *alluaudi* group of *Serrastruma,* for the mandibles are nearly or quite half the length of the head and have the basal five or six denticulae much coarser than the succeeding ones. In fact, *ludovici* can scarcely be differentiated from *alluaudi,* and may well prove to be a senior synonym of the latter when types can be directly compared.

Type locality. Southern Madagascar (Sikora).

SERRASTRUMA CALYPSO (Santschi) new combination

Strumigenys (*Cephaloxys*) *calypso* Santschi, 1923, Rev. Zool. Afr., **12:** 288–289, fig. 4a, worker, original description.

From Santschi's description and figure, this species seems virtually indistinguishable from Weber's *lotti.* An examination of the mandibular armature is needed to show whether or not the two are synonymous; in the latter case, the name *calypso* would take precedence. The type material of *calypso* is presumably in the Basle Museum. Dr. E. Handschin has written that he cannot lend material from the Santschi Collection because of catalogue difficulties.

Type locality. Ouha, British East Africa (Meyer).

Key to the sufficiently well known species of Serrastruma, based on the worker caste

1. Basal 5 or 6 denticulae of inner mandibular margin distinctly and suddenly larger, coarser, more acute and more irregular than those succeeding distally 2
   Basal 5 or 6 denticulae of inner mandibular margin not or only slightly and gradually enlarged, quite regular and with blunt apices (the first, basalmost denticle may be enlarged) 3
2. HL 0.55 mm. or more; body robust; ground pilosity of head variable, but usually more or less broadly spatulate; postpetiole swollen and broadly convex . . . . *alluaudi* (Santschi)
   HL less than 0.55 mm., usually less than 0.50 mm.; body slender; ground pilosity of head inconspicuous, narrowly spatulate; postpetiole small and narrowly convex . . . . *lotti* (Weber)
3. Propodeal teeth reduced to obtuse or rectangular vestiges . . . . *bequaerti* (Santschi)
   Propodeal teeth large or small, but always strongly acute 4
4. Pronotum with oblique or longitudinal costulate or striate sculpture, its punctulation absent or secondary 5
   Pronotum densely reticulate-punctulate like the mesonotum; costulation or striation absent or feeble and secondary to the punctulation 6
5. Costulation of pronotum fine, sharp, and close, longitudinal in direction (appearing like dense striation); ventral petiolar appendage vestigial, scarcely spongiform; cephalic ground pilosity broadly spatulate or spoon-shaped, very conspicuous, but short . . . . *maynei* (Forel)
   Costulation of pronotum loose and indefinite, largely oblique, with broad, usually shining interspaces; ventral appendage of petiole developed and spongiform; cephalic ground pilosity narrowly spatulate, not conspicuous *simoni* (Emery)
6. Larger form (HL 0.52–0.71 mm.) with narrower head (CI 77–83) and relatively longer mandibles (MI 37–42); funicular segments II and III always longer than broad . . . . *lujae* (Forel)
   Smaller form (HL 0.45–0.52 mm.) with broader head (CI 81–89) and relatively shorter mandibles (MI 34–39); segments II and III of funiculus not or just barely longer than broad . . . . *serrula* (Santschi)

Refer to *species inquirendae* section above for discussion of *ludovici* (Forel) and *calypso* (Santschi).

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THE CARABID BEETLES OF NEW GUINEA
PART 2. THE AGONINI

By P. J. Darlington, Jr.

With Four Plates

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
August, 1952

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No. 3.—*The Carabid Beetles of New Guinea.*[1] *Part 2. The Agonini*[2,3]

By P. J. Darlington, Jr.

CONTENTS

Page
Introduction 90
  Purpose; sources and disposition of material; acknowledgements 90
  Localities 91
  Methods, measurements, etc. 92
  Structures and characters 94
    The Tribe Agonini 94
    Form, color, microsculpture 95
    Head 95
    Prothorax 97
    Elytra 98
    Inner wings 100
    Lower surface 100
    Legs 101
    Secondary sexual characters 103
    Male copulatory organs 103
  Genera; nature of the New Guinean agonine fauna 105
  Evolution 107
    Loss of wings and setae; wing-and-seta formulae 107
    Reduction of eyes; tarsal lobes 108
    Adaptive nature of evolutionary trends 109
    Parallelism and convergence 110
    Role of geographical isolation 111
    Evidences of mutation 112
Taxonomic section 113
  Tribe Agonini 113
  Key to genera of Agonini of New Guinea 114
  Arhytinus 116
  Tarsagonum 120
  Euplenes 122
  Dicranoncus 124
  Lorostemma 125
  Notagonum 127
  Colpodes 158
  Plicagonum 173
  Lithagonum 176
  Iridagonum 181
  Altagonum 185

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[1] Work aided by grant of a fellowship by the John Simon Guggenheim Memorial Foundation, 1947–48; see page 91.

[2] The first part of this series is not yet published. See text for explanation.

[3] Manuscript received for publication December 20, 1951.

Maculagonum 213
Potamagonum 221
Gastragonum 222
Idiagonum 229
Montagonum 233
Nebriagonum 235
Laevagonum 243
Fortagonum 247

INTRODUCTION

Purpose; sources and disposition of material; acknowledgements. This paper is the first-published part of a taxonomic survey of the Carabidae of New Guinea. The survey should have some value of its own, will give an opportunity for the description of many new species which are on hand, and will make it possible to distribute much identified and paratype material for the use of other specialists, and the survey should yield also a few items of general zoögeographic and evolutionary interest. I have begun the survey with the tribe Agonini rather than with the tribes that come first on the list (the Junk-Schenkling Catalogue) because of my special interest in Agonini and because they form the principal part of the high-mountain carabid fauna in New Guinea.

The material used in this survey consists of three main collections: one made by myself from December 1943 to October 1944, and now in the Museum of Comparative Zoology; one made by Miss L. Evelyn Cheesman in 1933–34, 1936, and 1938 for the British Museum; and one made by Dr. L. J. Toxopeus during the course of the Netherlands Indian-American (Third Archbold) Expedition of 1938–39. My own New Guinean collection was made principally in two places: in the magnificent, diverse lowlands around Dobodura, Papua, during more than four months (March–July) when I was hospitalized there; and on the even more magnificent and diverse Bismarck Range, including 15,400 foot Mt. Wilhelm, which I was fortunate enough to be able to visit for two weeks of leave in October, through the kindness of the Australian administrators ("Angau"). The first set of my material is of course in the Museum of Comparative Zoology; duplicate sets are being widely distributed. Miss Cheesman's material includes a large number of otherwise unknown species, mostly from middle altitudes, from many localities widely scattered over New Guinea and from Japen and Waigeo Islands. This material is, of course, to be returned to the British Museum, except for a duplicate set which goes to the M. C. Z. Toxopeus' material is mostly from the Snow Mountains of Netherlands New Guinea and includes series of many fine species from high altitudes. This material was received from the Buitenzorg (Java) Museum. The first set of it, including holotypes and uniques, goes to the Leiden Museum; a good set goes to the Museum of Comparative Zoology by special arrangement, involving an exchange with the Buitenzorg Museum; and the balance is to be returned to the Buitenzorg Museum for further division. Besides these main collections I have had for study useful lots from the United States National Museum, the Muséum National d'Histoire Naturelle (Paris), the American Museum of Natural History (New York), the California Academy of Sciences, the Chicago Museum, the Bishop Museum, and the Hawaiian Sugar Planters' Association. (Some of the borrowed material has been from adjacent regions, for comparison, rather than from New Guinea itself.) I have received also either aid or specimens from a number of individuals whom I plan to name at the end of my work on New Guinean Carabidae rather than in the present first installment. All together I have had enough material to give at least clear outlines of the nature, distribution, and relationships of the New Guinean carabid fauna as a whole, a fauna which up to the present has been known in only a most fragmentary way.

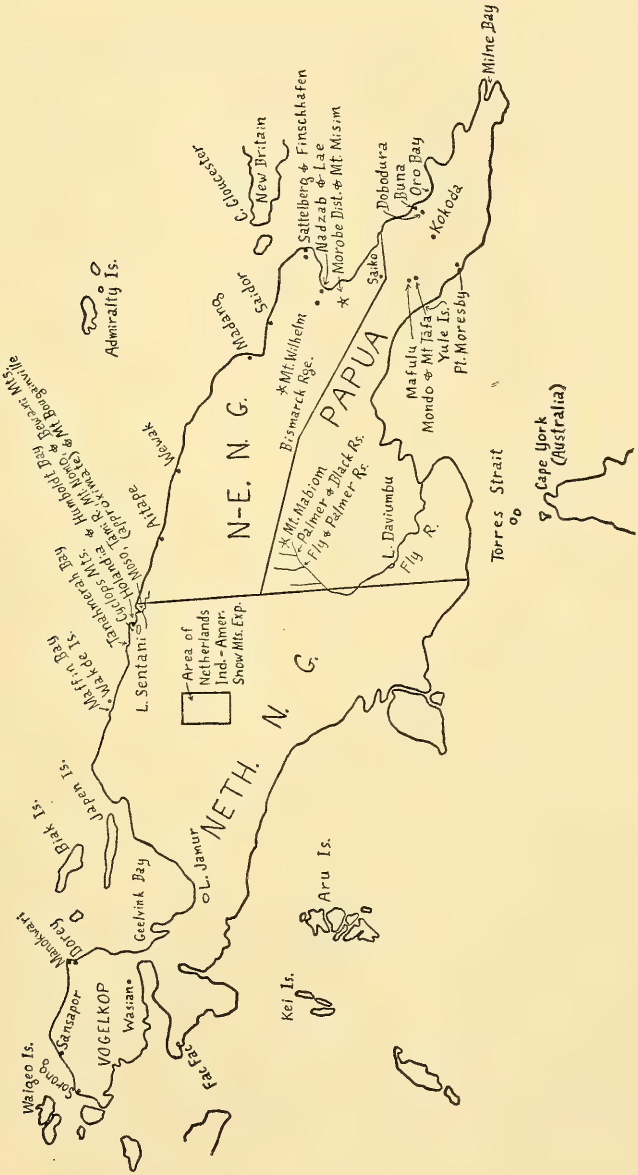
This paper has been written at the Museum of Comparative Zoology, but part of the groundwork for it was done at the British Museum, where, as holder of a John Simon Guggenheim Memorial Foundation Fellowship, I spent six months during the winter of 1947–48, studying the fine H. E. Andrewes Collection and other pertinent material in order to get a working knowledge of known Oriental and Indo-Australian Carabidae. I am very much indebted both to the Guggenheim Foundation and to the authorities and staff of the British Museum for this opportunity. I have a working knowledge also of Australian Carabidae, acquired as a result of a year spent in Australia with the Harvard Australian Expedition of 1931–32.

Localities. I see no need, or at least none now, for a formal gazetteer of localities referred to in this paper. They are not very numerous, and I have shown almost all of them on the preliminary outline map on page 93. In order to simplify the map, I have in a few cases not shown exact localities if they occur within definite, circumscribed areas that are indicated. For example I have not shown Miss Cheesman's exact localities in the Cyclops Mountains and on Japen and Waigeo Islands, nor those of Toxopeus in the Snow Mountains, nor mine on the Bismarck Range. Miss Cheesman has written at least two books about her travels in New Guinea, but unfortunately they are out of print and are very hard to obtain. The itinerary of Toxopeus' Snow-Mountain collecting is given by him in *Treubia*, Vol. 17, 1940, pp 271–279. A short gazetteer of localities, which should be useful t entomologists as well as herpetologists, will be found on pages 310–314 of Arthur Loveridge's recent paper on New Guinean reptiles and amphibians (*Bull. Museum of Comparative Zoölogy*, Vol. 101, No. 2, 1948). In spelling place names I have followed the National Geographic Society's map of Southeast Asia and the Pacific Islands (1944) for English names so far as they are given there, but have used the English rather than the Dutch names for well-known places in the Dutch areas. For example I have called the great mountain range of Netherlands New Guinea the Snow Mountains, not the "Sneeuw Gebergte". I have consistently referred to the three main political divisions of New Guinea as:

Papua
N-E. N. G. (North-east New Guinea)
Neth. N. G. (Netherlands New Guinea)

Methods, measurements, etc. Throughout this work I have used a modern Spencer stereoscopic microscope with, alternately, a two-tube fluorescent microscope lamp and a strong spotlight. I have rarely used a magnification of more than 54× (6 × 9), although the instrument will give 108× (6 × 18). The outline drawings of whole insects have been made under my direction by Mr. F. Y. Cheng, mostly with the use of a squared ocular. The other drawings have been made by myself with a camera lucida, then inked by Mr. Cheng, to whom I am much indebted for his painstaking work.

In drawing up descriptions I have tried to find a satisfactory compromise between the too-superficial work of many earlier authors and the too-laborious methods which, though theoretically desirable, are not practical in faunistic taxonomy. When possible I have based each description on one pair of average-looking specimens of a series, and have referred to the whole series to check only the more important characters. I have in each case made a set of standard measurements on the selected specimens with a micro-ruler in the microscope ocular, and from the measurements have derived three standard ratios of great value in distinguishing species. The ratios are: width of head to width of prothorax (given in the descriptions as head/prothorax, or as head .— width prothorax); width to length of prothorax (given as prothoracic width/length); and width of base to width of apex of prothorax (given as prothoracic base/apex). Width of head includes the eyes. Width of prothorax is greatest width. Length of prothorax is length at middle regardless of whether the anterior angles project forward. Width of base of prothorax is width between basal angles; of apex, between most advanced points of anterior angles. When either basal or anterior angles are obliterated, accurate measurement is impractical and the ratio of base/apex is given as an approximation.


Waigeo Is.
Sorong
Sansapor
VOGELKOP
Wasian
Manokwari
Dorey
Fak Fak
Kei Is.
Geelvink Bay
Biak Is.
Japen Is.
L. Jamur
NETH. N. G.
Aru Is.
Maffin Bay
Wakde Is.
Tanahmerah Bay
Cyclops Mts.
Hollandia
Moso, (approximate)
Tami R.
Mt Nomo
Humboldt Bay
Mt Bougainville
Bewani Mts.
L. Sentani
Area of Netherlands Ind.-Amer. Snow Mts. Exp.
Aitape
Wewak
N-E. N. G.
Mt. Mabiom
Palmer
Black Rs.
Fly
Palmer Rs.
L. Daviumbu
Fly R.
Torres Strait
Cape York (Australia)
Admiralty Is.
Madang
Saidor
Mt. Wilhelm
Bismarck Rge.
PAPUA
C. Gloucester
New Britain
Sattelberg
Finschhafen
Nadzab
Lae
Morobe Dist.
Mt. Misim
Saiko
Dobodura
Buna
Oro Bay
Kokoda
Mafulu
Mondo
Mt Tafa
Yule Is.
Pt. Moresby
Milne Bay

These ratios must be determined by measurements; they cannot be estimated satisfactorily by eye. It should be remembered, too, that the ratios vary somewhat in any given species and slight variations should not be given too much importance. In each case the specimens on which detailed measurements have been made and of which the proportions are given in the description are indicated in a special paragraph headed "*Measured specimens*". However, my statements of measurements of total length and width (see next paragraph) show the extremes of the entire available series of each species.

The measurements of total length represent specimens in fully extended natural position and include the elytral denticles or spines if present. In the case of specimens not actually fully extended I have measured separately, with a micro-ruler in the microscope, the elytra (from above, with the anterior part of the elytral disc level), the prothorax, and the head, and have added the fractional measurements together. The resulting total lengths are more accurate and more uniform and therefore more significant than those given by most earlier writers on Carabidae. Measurements of width have been made across the closed elytra at widest point. When, as is often the case, the elytra are slightly separated, the width of separation has been subtracted from the measurement. When the elytra are widely separated or warped, width has been given only approximately.

Some further notes on methods are included in the following paragraphs.

Structures and characters: the tribe Agonini. The tribe Agonini (Platynini or Anchomenini) is a well-recognized group, although different authors have set different limits to it. The New Guinean forms of the group are diverse, but all of them seem to be true members of the tribe in a fairly strict sense. They are distinguished from Pterostichini primarily by having the outer elytral margin not interrupted by an inner, subapical elytral plica. This interruption is absent in all Agonini, so far as I know[1]. However, though present and very distinct in most Pterostichini, the interruption is indistinct or absent in at least a few of those of the Australian Region. In doubtful cases the form of the parameres of the male copulatory organs is useful in separating the tribes. In most or perhaps all Pterostichini the left and right parameres are very unequal in size and shape; in all genera of Agonini that occur in New Guinea the parameres, though by no means equal, are much less differentiated (see Figs. 20-66).

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[1] Andrewes (*Trans. Ent. Soc. London*, Vol. 78, 1930, p. 40; and *Jour. Federated Malay Museums* Vol. 16, 1931, p. 451) mentions the presence of an internal elytral plica in *Aparupa* and *Idiastes*, both of which I consider true Agonini, but in these cases the plica does not interrupt the elytral margin as it almost always does in Pterostichini.

The following discussion is not a definition of the tribe Agonini but an analysis of some structures and characters of the New Guinean members of the tribe. The generic and specific descriptions of this paper will be modeled on the order of this discussion. Characters normal for a given genus will usually not be repeated under the species.

Form, color, microsculpture. The Agonini of New Guinea vary in size from 4.0 (*Arhytinus granum n. sp.*) to 23.0 millimeters (*Colpodes rex n. sp.*). They vary in form from *Bembidion-*, *Agonum-*, or *Platynus*-like to broadly oval or subquadrate, and in convexity from strongly depressed to very convex or with inflated elytra. A strikingly fusiform shape has been evolved apparently independently in certain (but not all) species of several different genera (*Maculagonum, Iridagonum, Altagonum,* and *Fortagonum*), and a subfusiform or *Amara*-like shape has been evolved in several additional stocks. The color is usually black or brown; less often at least partly, especially on elytra, purple, blue, or green (*Euplenes,* several *Colpodes, Altagonum cheesmani* and *regiscapha,* and *Fortagonum limum*); and rarely the elytra are blue or green with yellow blotches (*Euplenes laetus*) or red tips (*Euplenes apicalis* and *Colpodes laetus*). In *Maculagonum* the elytra, though not metallic, are mottled or blotched with dark and pale. A majority of the species of New Guinean agonines are not iridescent, but a good many scattered through a number of different genera are faintly so at least on elytra in strong light, and a few (especially the species of *Iridagonum*) are strongly iridescent. The upper surface varies in sculpture but is rarely coarsely or extensively punctate. Reticulate microsculpture is almost always present (absent or nearly so only in *Lithagonum* and in *Gastragonum laevisculptum*) but varies in distinctness and in size, shape, and depth of meshes. In the descriptions the microsculpture is said to be normal when the meshes are visible in good light at a magnification of 54×, and when they are isodiametric on head, moderately transverse on pronotum, and equally or more transverse on elytra. Many departures from this normal pattern are described under different species below. Generally speaking, so far as New Guinean Agonini go, characters derived from the microsculpture are of no more than specific and sometimes of less value. In several cases distinct differences in microsculpture separate geographical subspecies which are otherwise indistinguishable or nearly so.

The head in different New Guinean Agonini varies from rather short to more or less elongate, and from slightly less than half as wide to fully as wide as the prothorax. The mandibles are only moderately long and rather strongly curved except in certain species of *Fortagonum* (*forceps* and *cychriceps*) in which they are much longer, more slender, and straighter than usual. The eyes are often large and prominent, but also often reduced in both size and prominence, and rarely (*Laevagonum citum, Fortagonum cychriceps*) so small and flat as scarcely to break the outline of the sides of the head. In several independent cases the eyes, though much reduced in size, are still more or less abruptly prominent, sometimes abnormally and strikingly so. This is the case in one species of *Notagonum* (*reversior*), one of *Iridagonum* (*subfusum*), one of *Maculagonum* (*setipox*), one of *Gastragonum* (*laevisculptum*), all four species of *Idiagonum*, some *Nebriagonum*, the single known species of *Montagonum*, and some *Fortagonum*, especially *Fortagonum limum*, in which the eyes are not only abnormally abruptly prominent but also set off above from the front of the head by deep channels. More or less similar, small but very abrupt "popped" eyes occur in some other Oriental Agonini, including the genotype of *Colpodes* (*brunneus* Macl.), some other species of *Colpodes* (*aeneipennis* Dej., *sjostedti* Andr., and *latus* Louwerens), and all three species of the Himalayan genus *Aparupa* Andr. The eyes are not equally abrupt in all of the New Guinean forms listed above, but in each case they are much more so than in closely related forms. This peculiar modification of the eyes may be an adaptation, but it seems more likely that it is merely a secondary mutational effect which occasionally, but not usually, accompanies reduction of eyes, and which is obviously not necessarily of much phylogenetic significance. The usual two supraocular setae are present above each eye in most New Guinean Agonini. The posterior pair of the setae is about between the posterior edges of the eyes when the latter are normally large and prominent, but more or less behind the level of the posterior edges of the eyes when the latter are much reduced. This is a useful taxonomic character in some cases. The anterior supraocular setae have been lost in three probably independent cases: in one species of *Iridagonum* (*subfusum*), one of *Nebriagonum* (*percephalum*), and the entire genus *Fortagonum;* and in *Fortagonum bufo* the posterior as well as the anterior supraocular setae have been lost. It should be added that, in the case of *Nebriagonum percephalum*, although the anterior supraocular setae are absent in eleven specimens, the right anterior seta (but not the left one) is present in the twelfth specimen. Of course in the case of these and other fixed setae the setae themselves are often broken off, but their position is shown by strong punctures. The punctures as well as the setae are absent in the cases listed above. The antennae of different New Guinean Agonini vary in length and thickness of segments, but are always more or less normal in structure, with dense pubescence beginning near the base of the fourth segment. I have not taken taxonomic characters from the antennae and have usually not mentioned them in the descriptions. The neck in some cases is and in others is not impressed above. The front is usually more or less evenly convex with a pair of variable but usually slight anterior impressions. I have called this condition normal; variations from it are noted in the descriptions. The mentum is usually toothed, but the tooth is absent in *Arhytinus* and is either absent or broken off in one species of *Colpodes* (*sinuicauda,* represented by two specimens, both of which lack a mentum tooth). When present, the mentum tooth is triangular, varying in exact form in different species, with the apex pointed, rounded, more or less truncate, or slightly emarginate. Some of this variation occurs within single species as well as between species. In general I have not found the form of the mentum tooth useful in taxonomy of New Guinean Agonini, and I have usually not mentioned it in the descriptions. This is true also of the other mouth parts. In general I have not found them useful in the present study, and I have therefore omitted them from the descriptions.

The prothorax in different New Guinean Agonini varies greatly in form, proportions, and other details. No general discussion of the details is necessary except in the case of the lateral pronotal setae. There are normally two setae on each side of the pronotum, on or near the lateral margin, one (the anterior-lateral seta) near or before the middle of the prothoracic length, the other (the posterior-lateral seta) at or near the base. Both pairs (anterior and posterior) of these setae are uniformly present in the first eight genera (through *Plicagonum*) here treated, in all the species of *Gastragonum* and *Idiagonum,* and also in *Maculagonum setipox* and most specimens of *Nebriagonum cephalum,* although all the other species of the two last-named genera have lost one or both pairs of the setae. One or both pairs are absent also in all New Guinean Agonini not named above. A few have lost the posterior-lateral setae but not the anterior-lateral ones (*Lithagonum,* some specimens of *Nebriagonum cephalum,* and both known specimens of *Laevagonum subcitum*). More often the anterior but not the posterior pair has been lost (*Iridagonum,* most *Altagonum,* most *Maculagonum, Montagonum*). And in the remaining cases both pairs of the setae are lost (*Altagonum nudicolle* and *fatuum, Potamagonum,* most *Nebriagonum,* most *Laevagonum,* all *Fortagonum*). The preceding lists suggest what is certainly the case, that presence or absence of one or both pairs of lateral pronotal setae is not necessarily of itself an important taxonomic character. In fact in *Nebriagonum cephalum* the posterior-lateral setae are present or absent, or sometimes present on one side only, in different specimens of the type series. Nevertheless, in many other cases presence or absence of these setae does give a useful "tag" for the identification of species or genera. These setae, like the supraocular ones, are often broken off, but then their former presence is shown by characteristic punctures which are absent when the setae have failed to develop. A formula for indicating presence or absence of the standard supraocular and lateral pronotal setae is described below, under the heading "Evolution". The disc of the pronotum is described as normal when it is moderately convex and has a more or less impressed, more or less abbreviated, fine, median longitudinal line, and two less sharply defined but distinct transverse impressions near the apex and base respectively. The actual apex and base sometimes are and sometimes are not margined by fine impressed lines.

The elytra of different New Guinean Agonini differ greatly in form and proportions, and also in many details which yield good taxonomic characters. The elytral disc is in some cases regularly convex and in others more or less impressed before the middle. This character is surprisingly constant in some species and is useful especially in superficial recognition of certain *Notagonum.* The bases of the elytra are usually entirely margined to or nearly to the scutellum, but the margin is incomplete inwardly in a few cases (*Tarsagonum, Colpodes acuticauda, Idiagonum, Fortagonum cychriceps*). At the humeri the marginal line is in some cases rounded and in others angulate, the angles being obtuse, right, or acute in different cases; generally speaking the angles are rounded or obtuse in species with normally formed elytra, more nearly right or acute in those with elytra oval or the whole body oval. The lateral margins or gutters of the elytra vary in width in different species. The lateral margins posteriorly, just before the subapical sinuations, are usually rounded, but in a few cases are abruptly angulate or even with very short spines (*Notagonum externum, Colpodes saphyrinus sloanei, Colpodes antedens*). The subapical sinuations are usually moderate or strong but in some cases slight or absent. The form of the subapical sinuations, or their absence, is usually a specific rather than a generic character, although it is more or less constant in some small genera. The apices themselves vary extremely in form (conjointly or independently rounded, subtruncate, angulate, or slightly produced), and are dentate or spined in a number of taxonomically diverse species. Well developed spines occur in *Tarsagonum latipes; Notagonum subrufum* and *spinulum; Colpodes violaceus, saphyrinus sloanei,* and *antedens; Altagonum tutum, cheesmani,* and some specimens of *scapha*; and shorter spines occur in some other species, including some specimens of *Potamagonum diaphanum* and *Nebriagonum arboreum.* Spines seem to have been evolved *independently* in each of the species named. The apical elytral spines vary in position in different species; they may be opposite the ends of the fourth, third, second, or sutural intervals. The sutural angles of the elytra are only rarely actually spined but they are very often denticulate, the denticles being in some cases prominent and in others inconspicuous. Sometimes the denticles vary in development or are even present or absent in single populations. Also, they sometimes vary with angle of view. When the denticles are only slightly developed they are likely to appear distinct if seen from in front of the perpendicular, indistinct if seen from farther back. Among the Agonini of New Guinea the presence or absence of these denticles is often useful to distinguish species, but rarely genera. The character is obviously one which should be used with discretion. The striation of the elytra is entire or nearly so, and the sutural striae are long, in all New Guinean Agonini. The striae are usually impunctate or nearly so, rarely coarsely punctate. In some cases the edges of the striae are slightly irregular although no distinct punctation can be distinguished. In these cases I have described the striae as "not distinctly punctate" or "indistinctly punctulate". The striae vary in depth, and the intervals, therefore, in convexity. The outer intervals, especially the eighth and ninth and sometimes also the seventh, are in some cases variously modified toward apex. In most cases they end or fuse without noteworthy modification other than a moderate narrowing of the eighth and widening of the ninth interval toward apex. In these cases I have described these intervals as "not much modified toward apex". In other cases their form is described in detail. The eighth and to a less extent the seventh intervals are sometimes much compressed toward apex (*Colpodes bennigseni*), or longitudinally impressed or sulcate (*Tarsagonum latipes*, *Colpodes acuticauda*, all species of *Iridagonum* except *quadripunctellum*, *Altagonum pallinox*, *A. sphodrum* etc., and some specimens of *Fortagonum fortellum*). The ninth or normal submarginal interval, which is usually somewhat widened (and more or less interrupted) toward the apex, is sometimes abnormally narrow and convex, or longitudinally impressed. In certain cases the marginal channel itself is more or less modified especially posteriorly, being sometimes abnormally wide and flat (*Fortagonum cychriceps*) or with its inner part swollen and forming posteriorly a more or less distinct extra or tenth interval. Such a partial or fragmentary tenth interval is characteristic of the entire genus *Idiagonum* and is more or less developed in several species of *Fortagonum*. *Fortagonum fortellum* is remarkable for the variation of its outer elytral intervals, which are sometimes not much modified toward apex, sometimes strongly longitudinally impressed; and in this species a short but well defined fragment of an extra tenth interval is present in some specimens but not in others (these variations are all in one series from a single small strip of mountain forest). The third elytral interval normally has three dorsal punctures, each bearing a rather inconspicuous seta. The punctures are usually more or less evenly spaced along the length of the elytron, about ¼ from base, near middle, and about ¼ from apex; the first is usually near the third stria, the others, near the second one. When the punctures are arranged in about this way, the third interval is said in the following descriptions to be normally 3-punctate. Many departures from the normal condition, involving differences in position of, or loss of one, two, or all of the punctures, are noted in the descriptions of different species. In some cases loss of one or more punctures is a constant character useful in defining species. For example in the first species-group of *Altagonum* and in *Iridagonum* some species have the third elytral interval always 3-punctate, others, always 2-punctate, with the anterior puncture missing. In other cases, however, the occurrence of punctures on the third interval is extremely variable in single species (see descriptions of *Nebriagonum cephalum* and *Fortagonum fortellum*).

The inner wings vary in New Guinean Agonini, being in some cases fully developed, in others vestigial. I am well aware that such variation is often of little importance among Carabidae. However it so happens that in New Guinea there is only one agonine genus in which the wings are variable. This is *Gastragonum*, which includes species which, so far as my material goes, are fully winged, others which are vestigially winged, and one (*terrestre*) which is dimorphic. In every other genus here treated the wings are either uniformly full or uniformly vestigial in all my New Guinean material. Under these circumstances the state of the wings becomes a very useful taxonomic character. When the wings are vestigial, the metepisterna are often more or less shortened. This character has been overstressed in the past, especially in classifications of *Colpodes*. I shall use it very little here.

The lower surface is usually impunctate or virtually so in New Guinean Agonini, except of course for the presence of certain "fixed" setigerous punctures, but in a few cases the lower surface is more or less extensively punctate especially at the sides. The abdomen usually lacks pubescence other than fixed setae, but in about ten separate cases scattered pubescence is present either localized on some part of the abdomen (usually near middle of base) or over much or all of it. The cases are: (1) *Arhytinus*, in which scattered pubescence seems to be confined to the last ventral segment of the female only; (2) *Notagonum angustellum*, *subnigrum*, and *vile*, in which the abdomen is extensively pubescent, though not equally so in all the species named; (3) *Notagonum externum*, with a very little fine pubescence near middle of abdomen; (4) *Notagonum sinuum* and *vaporum*, in which abdominal pubescence is again extensive; (5) *Notagonum subimpressum,* in which the pubescence is slight and mostly near the middle; (6) *Colpodes acuticauda,* with a little fine and irregular pubescence; (7) *Lithagonum,* with abdomen rather variably and sparsely pubescent; (8) *Altagonum pubinox, pallinox, noctellum,* and *planinox;* (9) *Altagonum sphodrum* and *postsulcatum*; (10) *Gastragonum laevisculptum.* I think that pubescence has appeared on the abdomen *independently* in most or all of these ten cases. The prosternal process in New Guinean Agonini is as a rule simple: not margined nor tuberculate at tip, not setose, and with the posterior declivity not strongly compressed, though sometimes moderately so. Exceptions to this rule are noted in the descriptions. The principal exceptions are that the tip of the prosternal process is margined or tuberculate in *Tarsagonum latipes* and *Fortagonum bufo,* and setose in all four species of *Idiagonum.* The mesepimera are usually very narrowly triangular, but are somewhat wider, with outer margin about one-half as long as the anterior one, in *Euplenes.* This is correlated with and probably a result of evolution of a rather broad and depressed body-form in *Euplenes.* The metepisterna vary with the state of the wings, and have already been mentioned in that connection.

The legs are more or less normally formed in all New Guinean Agonini but vary in many details, of which I shall mention only those found useful in taxonomy in the present paper. It is likely that many other details, including the presence or absence of certain setae on the femora and the clothing of the lower surface of the tarsi, may eventually prove of great taxonomic value, but they may perhaps be more profitably studied in some connection other than the present one, preferably in the course of a world-wide classification of agonine genera. The following discussion is, for practical reasons, limited to the hind tibiae and tarsi and applies to the Agonini of New Guinea only. The hind tibiae are deeply sulcate along their extreme outer edges in *Tarsagonum* only. The hind tarsi, though variable, are usually more or less slender, but are somewhat wider than usual and symmetrical in *Euplenes,* and wide and asymmetrical in *Tarsagonum.* The first three or four segements of the hind tarsi are usually more or less grooved on each side above. The presence or absence and the depth of the grooves can be used in taxonomy, but the characters are difficult both to see and to describe accurately, and I have therefore usually avoided them here. They have been much over-used in the past. The form of the fourth segment of the hind tarsi is variable and is important in agonine taxonomy, though not so important as it has been thought to be. This segment may be simply emarginate at apex or with short or moderate or long apical lobes below (see Figs. 16–19). When lobes are present, the outer one is usually longer than the inner, but the two are nearly equal in *Euplenes*. In observing the shape of the fourth hind-tarsal segment, great care should be taken not to mistake a middle tarsus for a hind one and to see both sides of the fourth segment clearly so as not to overlook a lobe that may be hidden below the base of the fifth segment. There is a definite correlation between the form of the fourth hind-tarsal segment and the habitats or habits of different agonines. The segment tends to be simply emarginate in ground-living species, lobed in arboreal species and in those that live beside running water, but there are many exceptions to this general rule. As might be expected in view of the apparently adaptive nature of its modifications, the fourth hind-tarsal segment is not really fundamental in agonine taxonomy. The shape of this segment does not, or at least not usually, define large and diverse genera such as *Colpodes*, although it is more or less constant in many smaller genera. In the New Guinean genera, the fourth hind-tarsal segment is emarginate in *Arhytinus*; strongly but very asymmetrically lobed in *Tarsagonum*; strongly and symmetrically lobed in *Euplenes;* asymmetrically lobed in *Dicranoncus*; emarginate in *Lorostemma*; variable (emarginate in several stocks and more or less lobed in several others) in *Notagonum*; variable also in *Colpodes*, briefly lobed in *Plicagonum*, rather briefly lobed in *Lithagonum*; emarginate in *Iridagonum*; usually simply emarginate in *Altagonum* but with short lobes in four species which are probably not directly related to each other (*caducum, cheesmani, scapha, nudicolle*); emarginate in *Maculagonum*; briefly lobed in *Potamagonum*; variable in *Gastragonum*; emarginate in *Idiagonum*; variable in *Nebriagonum*; emarginate in *Laevagonum*; emarginate in *Montagonum*; and variable in *Fortagonum*. I give this list in full to emphasize the variability of this character so far as New Guinean agonines are concerned. The fifth segment of the hind tarsi sometimes does and sometimes does not have a row of conspicuous "accessory setae" on each side of its lower edge. The presence or absence of these setae is an important taxonomic character, but it again is not so important as has been thought. The setae are absent or only rudimentary in most New Guinean agonines but are more or less obvious in a few: *Euplenes*, (*Dicranoncus*), two *Colpodes* which are probably not directly related to each other (*s. sloanei, antedens*), *Potamagonum*, and some *Nebriagonum* (see notes under this genus). Their somewhat erratic occurrence and the fact that they are not equally developed in the different forms listed show that presence of obvious accessory setae on the fifth hind-tarsal segment is not necessarily a character of full generic value. This conclusion is reinforced by another fact. Although only a few of the New Guinean species of the tribe have the accessory setae well or even moderately well developed, very many of the species, perhaps even most or all of them, have the setae present in a rudimentary form, as very short, fine hairs barely visible in clean specimens at 54× with good light. I do not know whether these minute hairs are vestiges indicating the presence of longer setae in the ancestral stocks from which most or all existing New Guinean agonines have been derived, or whether they are parts of minute sensory organs or other structures normally present in Agonini, from which larger setae may be evolved. In either case the presence of minute hairs in so many forms lessens the significance of the occurrence of more or less enlarged setae in a few forms. The tarsal claws are simple in all the agonines now known from New Guinea, but each claw has an acute tooth below at base in *Dicranoncus*, of which one species may occur on the island. The sole of the first four hind-tarsal segments is variably clothed or margined with hairs or bristles in different Agonini, and the variations will probably be useful in taxonomy, but I have not attempted to use them in the present paper, except as an aid to distinguishing *Lorostemma* from *Notagonum*.

The secondary sexual characters of New Guinean Agonini are in general those which are normal for the tribe in other parts of the world: the front tarsi are slightly dilated in the male, with the first three segments biseriately squammulose beneath; and the last ventral segment bears one seta on each side in the male, two on each side in the female. The modification of the front tarsi of the male occurs in all New Guinean Agonini so far as my material goes. However there are a few exceptions to the normal in occurrence of ventral setae: in *Notagonum altum* the female usually has only one seta on each side of the last ventral segment, like the male; in *Colpodes rex*, the male has one, the female usually three such setae on each side; and in *Lithagonum* the male has usually two or more (not one) and the female usually four or more (not two) setae on each side. Two other, minor external sexual differences appear in single genera of New Guinean agonines. In *Arhytinus* the last ventral segment is glabrous in the male (except for the conspicuous setae mentioned above), sparsely and inconspicuously pubescent in the female. And in *Maculagonum* the last ventral segment is moderately or strongly emarginate at apex in the male, entire in the female. This character appears also in a less marked form in a few other species of New Guinean agonines, but in most cases the last ventral is entire or nearly so in both sexes.

The male copulatory organs of some Agonini present good characters which define major groups within the tribe. In certain genera which do not occur in New Guinea (*Calathus*, *Sphodrus*, etc.) the right paramere is distinctively long and slender, not relatively short and spatulate as it is in *Agonum* (*cf.* Jeannel, *Faune de France, Coléoptères Carabiques,* Part 2, 1942). However, I have found no such obvious group character among New Guinean agonines, all of which have copulatory organs of the general *Agonum* type, with the right paramere more or less smaller than the left one, both being simply oval or spatulate. There are many small variations in the form of the apex of the middle lobe which, after adequate study of series to determine individual variation (which is sometimes considerable), might be used to define species, and there are also differences in the armament of the internal sac which, in different New Guinean agonines, may bear a conspicuous hook (*Tarsagonum latipes*), or a few or many small spines (*Arhytinus major, Notagonum reversior, Colpodes antedens,* and others), or thickened areas (*Plicagonum rugiceps,* etc.), or (most commonly) no conspicuous armament but inconspicuous areas of minute bristles or granules. There are undoubtedly specific and generic characters to be found in these differences, although they are not always so important as they seem at first glance. However, I have not tried to use them here. To study them properly would require too much time in proportion to the probable results so far as the classification of the Agonini of New Guinea alone is concerned. Other characters are so numerous and so good among New Guinean agonines that the genitalic ones are hardly necessary. The basic genitalic characters of different groups of Agonini should be worked out as part of a study of the phylogeny and classification of the tribe for the whole world. Some day I hope to make such a study. In the meantime, I do not know which of the many details of the agonine copulatory apparatus should be stressed in drawings and I do not know from what angle the drawings had best be made, so the labor of drawing every species now might be wasted. However, for the information of specialists, I have figured (Figs. 20–66) the male copulatory organs of at least one species of each genus treated, of genotypes of all new genera except *Maculagonum* (of which another species is figured), of all new species of which only one male is known, and of a few other noteworthy species.

It is to be hoped that specialists will not make a habit of describing new forms of Agonini based only on small genitalic differences and especially not on differences which appear between my figures and their specimens. The figures have been made carefully, with a camera lucida, but they are not perfect. Carabid copulatory organs are very difficult to figure definitively. Some details are entirely without significance. For example, the dorsal (convex) profile of the middle lobe varies with the position of the movable internal sac. Many other details seem different from different points of view. This is especially true of the parameres, which are often not flat but curved or warped so that their outlines vary with angle of view; and whether or not the basolateral forks of the parameres are visible depends on angle of view. The armament of the internal sac is even more difficult to show accurately, especially when (as is usually the case) the sac is not everted. Even when small genitalic differences do exist between specimens, their significance is often doubtful, for the male copulatory organs do vary in some species. Almost more than any other parts of the body, the male copulatory organs of Carabidae should be studied and their variations understood before they are used in taxonomy.

After the two preceding paragraphs were written, I discovered that the position of the internal sac of the male copulatory organs varies with the way the specimens are killed. If they are killed dry, by fumes of acetic ether for example, the sac is usually fully retracted within the middle lobe. In this position, the sacs of different specimens can be compared in detail. If the insects are killed in alcohol, however, as my New Guinean ones were, the sac is often partly but not completely everted, and more so in some specimens than in others. Under these conditions it is difficult or impossible to compare the sacs of different specimens properly. This is a very serious disadvantage of alcohol-killed material. It could probably be overcome by dry-killing the insects and then preserving them in alcohol.

Measurements of total length and of width, which are given at the beginning of the generic descriptions and at the end of the specific ones, have already been discussed above.

Genera; nature of the New Guinean agonine fauna. So far as the Agonini of New Guinea are concerned, there are no characters which, of themselves, are always of generic value. The preceding discussion should have made this fact clear. The basic criterion which I have tried to use for genera is actual relationship, as shown by a sum of characters. In practice I have usually treated as genera groups of species which seem to be closely related among themselves but much less closely related to any other species and all of which share at least two distinctive characters, one of which may be a distinctive form or appearance. In some cases I have given weight to continuity of variation; that is, I have included in one genus species which are very unlike if the differences between them are bridged by a more or less continuous series of intermediate species. A good example of this is discussed in the notes under the genus *Nebriagonum*. In a few cases I have made monotypic genera for single species which are very strongly characterized.

Use of these practical criteria has resulted in recognition of nineteen genera of Agonini in New Guinea, including one (*Dicranoncus*) which is not actually recorded from the island but probably occurs there.

Four of the nineteen are previously known, small, natural genera which are primarily Oriental in distribution. These are *Arhytinus, Euplenes, Dicranoncus,* and *Lorostemma.* Three others are genera of convenience, each containing a number of species not necessarily all related to each other but not sufficiently characterized to be set apart in separate small genera now. One of these genera of convenience is the well known *Colpodes,* here used in a somewhat restricted sense. The other two I am calling *Notagonum* (southern *Agonum*) and *Altagonum* (alticoline *Agonum*) respectively. The remaining twelve genera are new, small, apparently natural groups all of which are probably confined to New Guinea (one or two reach also adjacent small islands) and most of which are confined to the mountains of the island.

It is obvious that in general this fauna consists of three elements. First are several stocks which are shared with and in most cases probably derived from the Orient, including not only the four small genera first named above but also several stocks of *Colpodes* and possibly some of *Notagonum.* Then comes a mass of species (most of those of the composite genera *Notagonum* and *Altagonum* and some *Colpodes*) which, though not strongly enough characterized to form separate small genera now, represent stocks which are more or less endemic to New Guinea and which are apparently in the early stages of differentiation and radiation there. Finally there are the twelve smaller, endemic genera, most of which are probably derived directly from the composite groups but which are more differentiated and some of which have radiated on New Guinea or even on single mountain ranges of the island. This whole picture is clearly one of accumulation of a rather limited number of stocks apparently partly (but perhaps not wholly) from the Oriental Region, of preliminary differentiation and adaptation to different lowland and mountain habitats, and finally of evolution and radiation of a considerable number of more distinct endemic groups which I have called genera. As to when the different stocks reached New Guinea, about all that can be said is that they have probably arrived at different times. Some probably came long ago (but not necessarily all at the same time) but whether they arrived in the Tertiary or before it can hardly be said in the absence of a fossil record. Some others have probably come more or less recently. Some of them are still only specifically or subspecifically different from Oriental forms, and in two cases (*Colpodes laetus* and *C. bennigseni*) I have found no significant differences between Oriental and New Guinean specimens.

Two facts of general interest arise from this brief discussion of the New Guinean agonine fauna. The first is that the whole fauna of nineteen genera and one hundred and twenty-one species and subspecies is derived from comparatively few ancestors which have come, at least partly from the Orient, at different times, some of them probably very recently. The other fact of general interest is that the mountain agonines — and Agonini are the most numerous Carabidae on the higher mountains of New Guinea — seem to have evolved more or less in place, and at least in most cases to have been derived from stocks which still occur at lower altitudes in New Guinea. In other words, the mountain agonine fauna is in its origins an endemic one, not a relict one.

Evolution: loss of wings and setae; wing-and-seta formulae. Certain definite evolutionary trends are distinguishable among New Guinean Agonini, especially one toward loss of wings and of certain setae especially in mountain environments. I have discussed the adaptations of mountain Carabidae elsewhere (*Ecological Monographs*, Vol. 13, 1943, pp. 37-61), and have suggested (p. 39 of the paper cited) the terms +winged (+w) (plus-winged) and −winged (−w) (minus-winged) for Carabidae with and without fully developed wings, and ±winged (±w) (plus- or minus-winged) for dimorphically winged forms; and +'s and −'s can be used also to indicate presence or absence of the most important standard setae and dorsal elytral punctures of Agonini: the two pairs of supraocular setae, two pairs of lateral prothoracic setae, and three setigerous punctures of the third elytral interval. By arranging the signs in the order just given, formulae can be made up for the state of the wings and setae in different cases. For example in *Notagonum* and other genera in which the wings are always fully developed and all the standard setae and punctures are always present, the formula is +w, ++, ++, +++. In *Altagonum*, in which the wings are always fully developed, both pairs of supraocular setae always present, the anterior lateral pronotal setae always absent and the posterior lateral ones usually present but sometimes absent, and the punctures of the third elytral interval usually present but all sometimes absent, the formula is +w, ++, −(+), (+)(+)(+). The signs in parentheses show the normal condition in the genus, the parentheses indicate that exceptions occur. The ultimate stage in loss of wings and setae is reached in one species of *Fortagonum* (*bufo*) in which the formula is −w, −−, −−, −−−. The following list of genera of New Guinean Agonini is arranged as nearly as possible according to presence or absence of fully developed wings and setae. The list is phylogenetic, but only in a very general way. The actual evolution of the agonines in question must have been very complex, with many separate lines, and much parallelism or convergence of different lines. The taxonomic part of this paper will follow the order of this list. The list applies to the New Guinean fauna only. In some cases (*Dicranoncus, Colpodes*) the formulae given do not hold for certain species of the same genera outside of New Guinea. In some cases I shall abbreviate the formulae to show presence or absence of the standard setae of the head and pronotum only. For example the abbreviated formula ++, −− indicates that both pairs of supraocular setae are present, both pairs of lateral pronotal ones, absent.

Table 1: Genera of Agonini of New Guinea

Number of species plus additional subspecies (*e.g.* 25+5) in each genus given in parentheses; state of wings and presence or absence of standard supraocular and lateral pronotal setae and setigerous punctures of third elytral interval shown by formula described in text; principal altitudinal occurrence of each genus indicated.

Arhytinus	(3)	+w, ++, ++, +++	lowlands
Tarsagonum	(1)	+w, ++, ++, ++−	lowlands
Euplenes	(2)	+w, ++, ++, +++	lowlands and mountains
(*Dicranoncus*)	−	+w, ++, ++, +++	(lowlands)
Lorostemma	(1)	+w, ++, ++, +++	lowlands
Notagonum	(25+5)	+w, ++, ++, +++	lowlands, some in mountains
Colpodes	(11)	+w, ++, ++, (+) (+)+	lowlands and mountains
Plicagonum	(2)	+w, ++, ++, (+)++	mountains
Lithagonum	(1+4)	+w, ++, +−, +++	lowlands and mountains
Iridagonum	(4)	+w, (+)+, −+, (+)++	lowlands and mountains
Altagonum	(24+4)	+w, ++, −(+), (+) (+) (+)	mountains, few in lowlands
Maculagonum	(6+1)	+w, ++, (−)+, −(+)+	mountains
Potamagonum	(1)	+w, ++, −−, +++	mountains
Gastragonum	(6)	±w, ++, ++, +++	mountains
Idiagonum	(4)	−w, ++, ++, −−−	mountains
Montagonum	(1)	−w, ++, −+, +++	mountains
Nebriagonum	(6)	−w, (+)+, (−) (−), (−) (−) (−)	mountains
Laevagonum	(4)	−w, ++, (−)−, −−−	mountains
Fortagonum	(5)	−w, −(+), −−, (−) (−) (−)	mountains

Reduction of eyes; tarsal lobes. Besides a strong tendency toward atrophy of wings in mountain habitats, often followed by changes in shape of the elytra and shortening of the metepisterna, and besides the tendency toward loss of setae especially, but not exclusively, in mountain habitats, the Agonini of New Guinea show also tendencies toward reduction of eyes and toward loss of the lobes of the fourth hind-tarsal segment. The eyes have been much reduced only in mountain-living forms and usually, but not exclusively, in flightless ones. As the eyes have become smaller they have usually become also either flatter or more abruptly prominent, as already described above. The evolution or devolution of the tarsal lobes is harder to reduce to simple terms, partly because the condition of the lobes in the ancestral stocks is unknown. In some cases the lobes may have been enlarged rather than reduced during evolution of New Guinean groups. However it is certainly true that the fourth hind-tarsal segment is more or less lobed in the majority of lowland agonines in New Guinea and simply emarginate in the majority of mountain ones, and it seems safe to say that the general tendency has been toward loss of the lobes in mountain habitats.

Adaptive nature of evolutionary trends. All these tendencies are probably adaptive and, although I have stated them simply, they are probably very complex in fact. This is surely true of the atrophy of wings of mountain Carabidae, which I have discussed elsewhere (*op. cit.*). The wings may sometimes be lost because of direct selection against flight on mountain tops, but their loss is probably also often a complex adaptation to existence of small, dense populations in isolated, small, stable, cool, mountain areas. Actually, although the wings have probably atrophied in the past in several different groups of New Guinean Agonini, they seem rarely to have done so recently, for the wings are either uniformly fully developed or uniformly vestigial in every New Guinean agonine genus except *Gastragonum*. This is in striking contrast to the state of affairs among the Carabidae of the north-temperate zone, where wing dimorphism is much more common within genera and even within species, and where the dimorphism probably reflects the recent instability of climate and habitats. The relative stability of the climate of New Guinea is probably one of the factors that account for the relative stability of the wing-state of Carabidae there.

Loss of setae by Agonini is correlated with and evidently somehow a result of life in mountain habitats. A loss of setae like that which has occurred among the Agonini of New Guinea has occurred also among those of the mountains of the West Indies and among those of the mountainous Hawaiian Islands. So far as the wings and setae alone are concerned, the parallelisms between the New Guinean and West Indian agonines are striking, although in most cases there is obviously no direct relationship. In the West Indies as in New Guinea the formulae for different agonines vary from +w, ++, ++, +++ to (in "*Colpodes*" *puncticeps* Darl.) −w, −−, −−, −−−; and many forms show intermediate conditions, having lost either the anterior or the posterior or both pairs of lateral pronotal setae and in some cases also the anterior supraocular setae. Why mountain-living Agonini should so often lose these setae I cannot satisfactorily explain.

The setae are probably tactile, and the best guess I can make about their loss is that they tend to be lost when the need for them is lost. Possibly the setae are warning devices, useful where enemies such as ants and lizards are numerous, but which tend to lose their usefulness and to be lost in places, like high mountains, where ants, lizards, or other enemies are relatively few.

Reduction of eyes is apparently related to and perhaps a result of reduced activity and, often, loss of the power of flight. At least there is a strong general correlation, though not a complete one, between reduction of eyes and atrophy of wings in all Carabidae. Reduction of the tarsal lobes is presumably also adaptive, resulting perhaps from abandonment of arboreal or stream-side habitats or from reduction of activity or of speed of running.

Parallelism and convergence. Since the main evolutionary tendencies of New Guinean Agonini are at least in part adaptive, it is not surprising to find much parallelism or convergence in them. The wings, though more stable than in some north-temperate Carabidae, have probably atrophied several times in different groups of New Guinean agonines, and resulting changes in shape of elytra and shortening of metepisterna have probably occurred several times too. Loss of setae has certainly occurred independently many times. The eyes have been reduced many times, and the reduced eyes have assumed an abnormal prominence in about eight separate cases among New Guinean Agonini alone. The lobes of the fourth hind-tarsal segment seem to have undergone multiple evolution and atrophy too, although the details are not easy to trace. There is rather striking parallelism also in some other characters which are obviously or presumably adaptive: for example in body form (strikingly fusiform in isolated species in four different genera), in development of spines at apices of elytra (probably developed independently in at least eleven cases in New Guinean Agonini), and development of ventral abdominal pubescence (present in ten probably independent cases). It will be seen, as I have already intimated, that some of these parallelisms occur in characters that have been given great value — too great value — in past classifications of Agonini. For example the presence of lobes on the fourth hind-tarsal segment has long been used as a principal character to define *Colpodes*. The length of the metepisterna has been used as a principal character to divide *Colpodes* into major groups. And the presence or absence of fully developed wings and of supraocular and/or lateral pronotal setae has been taken as *of itself* of generic value among Hawaiian and some other Agonini. It can hardly be reiterated too often that none of these characters is necessarily important of itself. In each of the cases just cited the use of these characters has resulted in the making of unnatural, composite genera or groups within genera. The use of such composite "genera of convenience" was and in some cases still is excusable as a necessary stage in classification, but it is time that the composite groups were recognized for what they are, and so far as possible genera should be natural. They should be based on actual relationships as shown by the sums of many characters of which certain ones should be stressed, not because of their inherent importance, but because they do hold in a given case, so that they are convenient tags for identification.

Role of geographical isolation. Geographical isolation, or separation of different circumscribed populations, has obviously been important in speciation of Agonini in New Guinea. In fact I am convinced from personal acquaintance with many groups of Carabidae in several parts of the world that geographical isolation is almost always a prerequisite for multiplication of species in this family. This is shown by the usual pattern of distribution of closely related species, which usually occur in separate but neighboring areas, and also by the distribution of incipient species, or subspecies. The latter appear to be primarily geographical among Carabidae. Different populations or subpopulations which are indistinguishable except in one or two minor characters, and which sometimes intergrade even in those, seem always to inhabit separate areas. The subspecies is of course now usually defined as a geographical form, so that non-geographical variants cannot properly be called subspecies in any case, but this is beside the point. The point is that among New Guinean Agonini, and among Carabidae in general, populations that differ more or less constantly but only slightly from each other apparently always or almost always do occur in different areas rather than in different habitats in the same area. Among New Guinean Agonini, for example, I have recognized as subspecies a number of forms characterized only by slight but more or less constant differences in size, or proportions, or color, or iridescence, or microsculpture. These forms are all geographical. They occur in different parts of New Guinea, not in different habitats. I can say this with some assurance because I collected much of the material myself, and knew fairly well what I was getting when I collected it. I know of no case either among New Guinean Agonini or among other Carabidae in which such slightly differentiated forms, which seem to me to be incipient species, are segregated primarily by habitats rather than geographically. It is true that in some cases obviously related but distinct species belonging to single genera or groups within genera do occur in different habitats in single small areas. Two such cases are described in the present paper under the genera *Nebriagonum* and *Laevagonum,* in both of which radiation of species into different habitats seems to have occurred on or near the Bismarck Range. But in these and most other cases of the same sort, at least among Carabidae, the species are distinct ones. It is possible that they have arisen primarily as a result of ecological segregation, but it is also possible that they were first segregated geographically and that they have come together again and become adapted to different habitats only after becoming specifically distinct. The Bismarck Range is sufficiently broken up, and the mountain forest to which many of the Carabidae are confined is sufficiently divided into separate tracts, to allow initial geographical isolation of local forms.

Evidences of mutation. The role of mutation in wing-atrophy of Carabidae has long been suspected and is now pretty well proved. Mendelian inheritance of vestigial wings has been demonstrated by actual breeding of one species of carabid (see Lindroth, *Hereditas*, Vol. 32, 1946, pp. 37–40), and the mode of occurrence of wing-forms in many other dimorphic species is such as to leave little doubt that the dimorphism is mutational and Mendelian. In some cases the wings seem to have been reduced from a fully developed to a fixed vestigial form by a single mutation. In other cases the reduced wings are variable, and intergrades may occur between the fully developed and vestigial wing-forms. In these cases the reduced wings may be controlled by more than one mutation, or possibly by one mutation the effect of which is modified by physiological factors. The whole subject of carabid wing-dimorphism and atrophy, and its relation to habitat and distribution, is discussed in Lindroth's great work on "Fennoskandischen Carabidae" (Part III; *Medd. Göteborgs Mus. Zool.*, Avd. 122, 1949, pp. 335ff).

Mutation is probably involved also in loss of setae by Carabidae. I have elsewhere (*Mem. Soc. Cubana Hist. Nat.*, Vol. 11, 1937, p. 136) described a case of strict dimorphism of setae in the Cuban *Phloeoxena deälata* Darl., in which, in a series of 35 specimens from one small area (the summit forest of Pico Turquino), the anterior supraocular and the anterior-lateral pronotal setae are apparently inherited as a group, presumably in Mendelian fashion, both these pairs of setae being present or both absent in all individuals of the series. I have found no similar case of strict dimorphism of setae among New Guinean agonines, but nevertheless it seems likely that loss of setae in the latter has been by mutation. In a number of cases one or more pairs of standard setae or of elytral punctures are uniformly present in certain species of a genus and uniformly absent in other species, and in these cases a simple mutational change is suggested. In some other cases (*e.g.* that of the posterior-lateral pronotal setae of *Nebriagonum cephalum*) certain setae occur erratically or asymmetrically. These cases recall, but do not exactly parallel, the variably reduced wings of some Carabidae. It seems likely that such irregular disappearance of standard setae is due to mutation modified by physiological factors. Mutation may reduce the seta-forming potential to near a threshold, and minor physiological factors or even chance may then determine whether or not a certain seta is formed in a given individual. In accordance with this possibility are the facts that formation of fixed setae is usually an all-or-nothing matter (a given seta is usually either fully developed or completely absent, rarely reduced or vestigial); and that in some cases a given seta is fully formed on one side and completely absent on the other in single individuals.

Dimorphism following mutation is to be expected also in form of eyes, form of fourth hind-tarsal segment, form of microsculpture (which is known to be dimorphic in some Dytiscidae), details of male copulatory organs, and other structures of taxonomic importance, but I cannot now give clear examples from Carabidae. It is very important that taxonomists should look for and record cases of such dimorphism.

TAXONOMIC SECTION

Tribe AGONINI

Anchomenini Auct., including Sloane (Trans. Ent. Soc. London for 1923, p. 248) and Jeannel (Faune de France, Coléoptères Carabiques, Part 2, 1942, p. 867; and Coléoptères Carabiques de la Région Malgache, Part 2, 1948, p. 513).

Platynini Auct., including G. Horn (Trans. American Ent. Soc. 9, 1881, p. 141).

Agoni Csiki (Coleopterorum Catalogus, Carabidae, Harpalinae 5, 1931, p. 739).

This group, under the various names cited, is variously defined and limited by different authors. Its exact characters and limits need not be discussed here, however, for all the New Guinean forms referred to it are typical Agonini in a fairly narrow sense. I shall therefore proceed at once to a discussion of genera within the tribe.

The Agonini of the tropics, including those of the Oriental-Australian area, are badly in need of generic revision. Jeannel (1948, *op. cit.*, pp. 215–217) has indeed offered a classification of the "principal" Oriental genera of the tribe, but he has omitted at least nine genera which have long been known from the Oriental Region, including some which are peculiar to it; his classification is based in part on characters which are not really of generic value among Oriental Agonini — for example, on presence or absence of denticles at the sutural angles of the elytra; and the classification is marred also by outright errors. For example, his new genus *Nesiocolpodes* is defined in part by absence of accessory setae on the fifth hind-tarsal segment, but the assigned genotype (*Colpodes saphyrinus* Chd.) has such setae plainly, though not conspicuously, developed. Also, Jeannel has misidentified the genotype of *Colpodes* (*brunneus* Macl.), and has figured under this name (*op. cit.*, 1948, p. 514, Fig. 235a) an entirely different species, belonging to a different genus according to his own key. This classification is so superficial and so confused by error as to be of little use even for Oriental Agonini, and it is no use at all for the New Guinean forms.

The following key to the genera of Agonini of New Guinea is far from perfect but it has at least the merit of being a result of real study of many species. It is, of course, a preliminary contribution to agonine classification rather than a final arrangement of even the New Guinean forms. The key is designed primarily for identification and is not intended to be phylogenetic. A more nearly phylogenetic arrangement of genera has been suggested above (Table 1) but, as I have said, agonine phylogeny has been much too complex to reduce to a simple linear arrangement.

Key to the Genera of Agonini of New Guinea

1. Mentum not toothed; (small, broad, convex, *Bembidion*- or *Perigona*-like forms) (p. 116) . . . . *Arhytinus*

— Mentum toothed (except apparently in *Colpodes sinuicauda*, a large, *Platynus*-like species) 2

2. Tarsi wide, flat, with first 3 segments as well as 4th obviously asymmetrical; hind tibiae deeply sulcate along outer edges; (winged, elytra gibbous with basal margin incomplete and apices spined, etc.) (p. 120) . . . . *Tarsagonum*

— Tarsi narrower, with first 3 segments not obviously asymmetrical (but 4th segment often somewhat asymmetrically lobed); hind tibiae not or at most slightly sulcate along outer edges 3

3. Prosternal process with setae; (rather large, dull black, mountain-living forms, with vestigial wings, and with pronotum usually strongly transversely rugulose) (p. 229) . . . . *Idiagonum*

— Prosternal process without setae 4

4. Mesosternal epimera more broadly triangular, with outer edge about ½ length of anterior edge; 4th hind-tarsal segment with 2 long, nearly equal lobes; (small, broad, depressed, bicolored forms, with elytral apices broadly rounded) (p. 122) . . . . *Euplenes*

— Mesosternal epimera narrower; 4th hind-tarsal segment emarginate or lobed, but if with long lobes, outer lobe longer than inner 5

5. Tarsal claws each with an acute tooth at base; (rather slender, winged, prothorax suboval); (not recorded from New Guinea but may occur there) (p. 124) . . . . (*Dicranoncus*)

— Claws not toothed..6

6. Apices of elytra at least in part minutely subserrate or with projecting granules; (first 4 hind-tarsal segments with a nearly regular single row of bristles on each side below, but with middle of sole bare); (slightly aeneous, somewhat alutaceous, *Agonum*-like, with 4th hind-tarsal segment emarginate, not lobed) (p. 125)................*Lorostemma*

— Apices of elytra not subserrate or granulate; (clothing of lower surface of hind tarsi variable, but rarely as described above) (*Agonum* and *Colpodes* in a conventionally broad sense)..............................7

7. Wings full; all standard setae of head and pronotum present; elytra not mottled with light and dark.....................................8

— *Either* wings reduced; *or* one or more pairs of standard setae of head or pronotum absent; *or* (if wings full and all head and pronotal setae present) elytra mottled and ♂ last ventral segment notched at apex..11

8. Small (4.8–9.7 mm.), *Bembidion*-, *Agonum*-, or *Platynus*-like forms; not brightly colored (sometimes, but not usually, iridescent); (apices of elytra rounded, angulate, denticulate, or rarely spined in line with 3rd intervals); (most or all ground-living, many in lowlands, some in mountains)...9

— *Either* larger, more or less *Platynus*-like forms, *or* at least partly purple, green, or blue; (apices or elytra usually either denticulate or spined, with spines often nearly in line of sutural intervals); (mostly arboreal forms of low and middle altitudes, but some mountain species may be ground-living)..10

9. Only moderately convex (except in *gibbum*); eyes large and prominent with posterior supraocular setae not or not much behind line of their posterior margins (except in *reversior* eyes are smaller but abnormally prominent, with posterior supraocular setae well behind line of their posterior margins); (lowland and mountain forms) (p. 127)..*Notagonum*

— More convex; eyes smaller and less prominent, with posterior supraocular setae well behind line of their posterior edges; (mountain forms) (see Couplet 12)................................*Gastragonum* in part

10. Front not wrinkled; color (in New Guinean forms) metallic, bicolored, or black (p. 158)......................................*Colpodes*

— Front longitudinally wrinkled; color brown, elytra sometimes testaceous (p. 173)...*Plicagonum*

11. Elytra mottled or blotched with dark and pale; ♂ last ventral segment strongly notched at apex (p. 213)......................*Maculagonum*

— Elytra not mottled nor blotched (but sometimes broadly margined with pale); ♂ last ventral not or only slightly emarginate.............12

12. All standard supraocular and lateral pronotal setae present; (convex; eyes somewhat reduced; wings full or vestigial or dimorphic; head/prothorax .70 or less; 4th hind-tarsal segment emarginate, not lobed); (see also Couplet 9) (p. 222).................................*Gastragonum*

— At least 1 pair of lateral pronotal setae absent (except in some examples of *Nebriagonum cephalum*, in which head/prothorax is .90 or more and 4th hind-tarsal segment is lobed)..............................13

13. Wings full 14
— Wings vestigial 17
14. Standard setae of head and pronotum ++, +− (note anterior pronotal setae present, posterior ones absent); body extensively punctate above and below) (p. 176) . . . . *Lithagonum*
— Standard setae (+)+, −(+) (note anterior pronotal setae always absent, posterior ones usually present) 15
15. Elytra strongly iridescent; lower surface with sides of sterna extensively punctate; (standard setae (+)+, −+; see also description) (p. 181) . . *Iridagonum*
— Elytra not or only moderately iridescent; sides of sterna not or only slightly punctate 16
16. Elytral striae conspicuously interrupted; 5th hind-tarsal segment with well-developed accessory setae; (standard setae ++, −−; see also description) (p. 221) . . . . *Potamagonum*
— Striae not interrupted; 5th hind-tarsal segment without obvious accessory setae; (standard setae ++, −(+)) (p. 185) . . . . *Altagonum*
17. *Either* head very large (head/prothorax .90 or more) *or* 5th hind-tarsal segment with obvious accessory setae; (standard setae (+)+, (−) (−), but never ++, −+); (see also description) (p. 235) . . . . . *Nebriagonum*
— Head relatively narrower; 5th hind-tarsal segment without obvious regular accessory setae (but sometimes with 1 or 2 small adventitious ones) . . 18
18. Standard setae ++, −+, with posterior-lateral pronotal ones about ⅙ of prothoracic length before posterior angles (p. 233) . . . . . *Montagonum*
— Posterior-lateral pronotal setae absent 19
19. Standard setae ++, (−)−; small (5.5–8.4 mm.), slender (p. 243) . . . . . . *Laevagonum*
— Standard setae −(+), −−; larger (8.8–12.4 mm.), usually stouter (p. 247) . . . . *Fortagonum*

Genus ARHYTINUS Bates

Bates 1889, Ann. Soc. Ent. France (6) **9**, p. 278.
—— 1892, Ann. Mus. Civ. Genova (Genoa) **32**, p. 378.
Andrewes 1931, Jour. Federated Malay Museums **16**, p. 473.

Diagnosis. See key.

Description. None required here. For a detailed re-description of genus and genotype see Andrewes, *op. cit.*, pp. 473–4.

Genotype. A. bembidioides Bates.

Generic distribution. Sikkim, Burma, etc. to the Philippines and New Guinea.

Notes. Although this genus is very different in appearance from most Agonini, it is not so widely set apart structurally, and the male copulatory organs (Fig. 20) are typically agonine. The species of the genus are all very much alike except in size, color of legs and antennal bases, and minor details of proportions, etc. I shall therefore describe in full only one of the New Guinean species (*medius*) and shall compare the other two with it.

Key to the Species of Arhytinus of New Guinea

1. Larger (8.0 mm.); tip of each elytron forming a small, bluntly rectangular, *explanate* angle (p. 118) . . . . *major*
– Smaller (not over 7.1 mm.); tips (sutural angles) of elytra either narrowly rounded or angulate with angles not or scarcely prominent and not explanate 2
2. Size average in genus (5.7–7.1 mm.) (p. 117) . . . . *medius*
– Very small (4.0 mm.); (see also description) (p. 119) . . . . *granum*

ARHYTINUS MEDIUS n. sp.

Description. Form as usual in genus (very small and broad, with prothorax only moderately convex, elytra relatively more so); piceous-black, upper surface moderately shining, silky and slightly iridescent, lower surface and femora brownish-piceous, tibiae and tarsi paler, antennae irregularly brown; microsculpture nearly normal: heavy and isodiametric to transverse on head, strongly transverse on pronotum, finer (just visible at 54×) and strongly transverse on elytra. *Head* rather short (as usual in genus); head/prothorax .74 & .79; eyes large and prominent; 2 supraocular setae each side, the first in a conspicuous pit, the second near inner posterior edge of eye; antennae stout (as usual in genus), outer segments about 2× long as wide (slightly variable); front with a pair of widely separated, round, poorly defined impressions anteriorly, just behind clypeal suture; front not otherwise impressed; mentum tooth absent. *Prothorax* wide; width/length 1.61 & 1.62; base/apex 1.18 & 1.13; sides arcuate for much of length, nearly straight and rather strongly converging posteriorly, not or slightly sinuate before posterior angles; latter obtuse but distinct; lateral margins rather narrow, wider posteriorly, flat, each with usual 2 setae at anterior ⅓ and base; basal foveae flat (not impressed), they and area between them across base rather irregularly punctate; disc otherwise impunctate, normal; anterior marginal line entire, posterior one vague. *Elytra* moderately rounded at sides, rather strongly convex (as usual in genus); basal margin entire, rounded at humeri; lateral margins moderate; apices continuing curves of lateral margins (subapical sinuations absent) to near sutural angles; latter slightly variable, either narrowly rounded or subangulate, but without *explanate* angulations; striae entire, rather lightly (somewhat variably) impressed, punctulate; intervals nearly flat or slightly convex, impunctate; outer intervals not much modified toward apex; 3rd interval impunctate. *Inner wings* fully developed. *Lower surface* impunctate except for a few punctures at sides of meso- and metasterna; abdomen not pubescent except on last ventral segment of ♀; prosternal process simple; mesepimera very narrow; metepisterna moderately long. *Legs* normally formed; hind tibiae vaguely sulcate along outer edges (middle tibiae more distinctly so); hind tarsi slender, with 1st segment longer than next 2 together (by measurement); 4th segment emarginate at apex, not lobed; sole of hind tarsus with bristles irregular (or in 4 rows ?) on 1st segment, in 2 regular rows with middle of sole bare on 2nd to 4th segments; 5th segment without obvious accessory setae; claws simple. *Secondary sexual characters* normal, except last ventral segment glabrous in ♂ (except for usual pair of conspicuous setae), with sparse, short, inconspicuous pubescence in ♀. *Measurements:* length 5.7–7.1; width 2.4–3.0 mm.

Types. Holotype ♂ (M.C.Z. No. 28,586) and 3 paratypes from Dobodura, **Papua**, Mar.–July 1944 (Darlington), taken among dead leaves on the ground in forest; additional paratypes from **Neth. N. G.** as follows: 1, Hollandia, July–Sept. 1944 (Darlington); 2, Sabron, Cyclops Mts., 2,000 ft., June & July 1936 (Cheesman, British Mus.).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Dobodura.

Notes. This is very near the genotype (*Arhytinus bembidioides* Bates of Indo-China, etc.) and certain Philippine species (*philippinus* Jedl. and *piceus* Jedl., if these are recognizable), but it differs from all of them in color of legs, with femora dark rather than pale. (I have seen the types or authentic specimens of all the species in question.) This difference is of itself of no more than subspecific value, but I prefer to treat the New Guinean form as a species until the interrelationships of the others are better understood.

ARHYTINUS MAJOR n. sp.

Description. Almost the same as *medius* (preceding species) in form and color except legs and antennae almost entirely blackish; same in generic characters; but larger and differing in details noted in following abbreviated description. *Head* .73 width prothorax; about as in *medius* but antennae a little more slender, with outer segments slightly more than 2× long as wide. *Prothorax* slightly narrower (width/length 1.55) than in *medius*, less convex, with wider margins more nearly in plane of disc anteriorly but more reflexed posteriorly; base/apex 1.17; sides arcuate anteriorly, strongly converging posteriorly, faintly sinuate before obtuse but distinct posterior angles; basal foveae wide but only slightly impressed, they and basal area between them punctate; anterior marginal line nearly entire but vague at middle, posterior one indistinct. *Elytra* of about normal outline and convexity for genus but with sides a little straighter than usual before middle; sides posteriorly almost evenly rounded to suture, but apex of each elytron near suture with a small, bluntly rectangular, slightly reflexed or explanate projection; striae rather light, punctulate; intervals nearly flat on disc, slightly more convex toward sides and still more at extreme apex. *Inner wings* fully developed. *Lower surface, legs,* and *secondary sexual characters* (of ♂) as in *medius*. *Male copulatory organs* as figured (Fig. 20), typically agonine. *Measurements:* length 8.0; width 3.2 mm.

Type. Holotype ♂ (M.C.Z. No. 28,587) from Dobodura, **Papua**, Mar.–July 1944 (Darlington); unique.

Measured specimen. The holotype.

Notes. This species is about the size of *Arhytinus irideus* Jedl., of which I have seen the type from Mindanao (British Mus.) and a second specimen identified by myself from Borneo (borrowed from British Mus.). As compared with *irideus,* the present new species has a relatively smaller, narrower, less convex prothorax with less well-defined lateral margins and more strongly punctate foveae; and the elytral apices have minute projections which are not present in *irideus.*

ARHYTINUS GRANUM n. sp.

Description. Almost a miniature replica of *medius* in form; same in generic characters; about same in color and sculpture, except microsculpture especially of elytra relatively more distinct, and surface correspondingly less iridescent. *Head* .79 & .80 width prothorax; antennae even stouter than in *medius,* outer segments about 1½× long as wide. *Prothorax* slightly narrower (width/length 1.50 & 1.55), with slightly narrower base (base/apex 1.08 & 1.04) and perhaps slightly more convex pronotum, but otherwise as in *medius.* Elytra about as in *medius* but a little more deeply striate, with striae less distinctly punctulate; apices almost evenly conjointly rounded (as in some examples of *medius*). *Inner wings* fully developed. *Lower surface, legs,* and *secondary sexual characters* (♀) about as in *medius,* with last ventral segment of ♀ with similar sparse, short, inconspicuous pubescence. *Measurements:* length (both specimens) 4.0; width 1.6 mm.

Types. Holotype ♀ (M.C.Z. No. 28,588) from Dobodura, **Papua**, Mar.–July 1944 (Darlington), taken among dead leaves on the ground in forest; and 1 ♀ paratype from Aitape, **N-E. N. G.**, Aug. 1944 (Darlington), taken in heavily flooded, forested or formerly forested country.

Measured specimens. The types.

Notes. Distinguishable from *medius* by small size and details given above. It is smaller than *minimus* Jedl. of the Philippines and differs from it also in color of legs, with femora brownish-piceous rather than yellow. *Arhytinus granum* here described is probably the smallest known species of the whole tribe Agonini.

TARSAGONUM new genus

Diagnosis. Genus strongly characterized by inflated form, incomplete basal margins of elytra, all tibiae strongly sulcate along outer edges, prosternal process margined at tip, and especially by wide, flattened, asymmetrical middle and hind tarsi.

Description. Genus based on one species, so generic and specific characters not separable. See specific description.

Genotype. Tarsagonum latipes n. sp. (below).

Generic distribution. Known only from one locality in eastern New Guinea.

TARSAGONUM LATIPES n. sp.

Description. Form as figured (Fig. 1), like very stout *Platynus* but with more convex pronotum and inflated elytra; black, appendages blackish or dark-brown; upper surface moderately shining, silky or opalescent rather than iridescent, with microsculpture fine but visible at 54×, normal. *Head* moderately elongate, .71 & .73 width prothorax; eyes moderate in size, not very prominent; anterior supraocular setae near inner corners of eyes, posterior ones distinctly behind line of posterior edges of eyes; antennae only moderately long, pubescent from near base of 4th segment (as usual); 3rd segment longer than 4th, more than 2× length of 2nd; outer segments about 4× long as wide; frontal impressions sublinear, not sharply defined, strongly oblique, more or less connecting anterior supraocular punctures with a pair of widely separated punctures at clypeal suture; front impunctate; neck constriction moderate; mentum tooth strong, triangular, channeled; ligula broad, bisetose; paraglossae slender, much longer than ligula, separated from it well before its apex; palpi rather slender; 2nd segment of labial palpi bisetose. *Prothorax* subcordate; width/length 1.29 & 1.33; base/apex 1.21 & 1.15; sides strongly rounded through much of length, strongly sinuate near base; anterior angles only slightly advanced, blunted; posterior angles about right, sharply defined; lateral margins moderate, flat or slightly reflexed, each with usual 2 setae at about middle of length and base respectively; basal foveae poorly defined, only slightly impressed, nearly flat, closely and rather coarsely punctate, the punctation extending across base and along sides of pronotum to apex; disc of pronotum otherwise impunctate, normal; anterior marginal line more or less interrupted at middle, posterior one present at sides but obsolete at middle. *Elytra* wide, inflated; basal margin obsolete inside ends of 5th striae, broadly rounded at humeri; lateral margins narrow anteriorly, wider behind middle, then narrower to apices; subapical sinuations absent or indistinct; apices each with a spine about opposite 3rd interval (the spine about as long as width of 1½ discal intervals), then more or less emarginate to sutural angles; latter obtusely angulate, not denticulate; striae entire except some inner ones slightly abbreviated at base, finely punctulate; intervals flat or nearly so, not punctulate; 2nd interval slightly broader than others on disc; 8th narrowed toward apex, and both 8th and 9th impressed or longitudinally sulcate toward apex; ocellate puncture at base of 1st stria (as usual); anterior dorsal puncture of 3rd interval by 3rd stria at basal 1/10, middle dorsal puncture about midway between 2nd and 3rd striae just before middle of elytral length, posterior dorsal puncture absent in all specimens. *Inner wings* fully developed. *Lower surface* with sterna extensively and closely punctate, the punctation extending to sides of first 2 abdominal segments and grading into wrinkling at sides of following segments; abdomen impunctate in broad median area, not pubescent; prosternal process margined at tip but without setae; mesepimera narrow; metepisterna rather long. *Legs* normally formed; all tibiae strongly sulcate along outer edges; all tarsi broad, much flattened; segments 1 to 4 each more or less asymmetrical (Fig. 15), with 2 main sulci above and 2 less distinct ones at sides, so segments are more or less 3-costate above; segments 1 to 4 below densely bristly; 4th hind-tarsal segment with a long outer lobe but almost no inner one (Fig. 16); 5th hind-tarsal segment without obvious accessory setae; claws simple. *Secondary sexual characters* normal. *Male copulatory organs* as figured (Fig. 21). *Measurements:* length (including elytral spines) 10.6–11.6; width 4.6–4.9 mm.

Types. Holotype ♂ (M.C.Z. No. 28,589) and 12 paratypes all from Dobodura, **Papua**, Mar.–July 1944 (Darlington). All the specimens were found in masses of dead leaves on the ground in forest; most of them, in a single deep, damp bed of such leaves under the top of a fallen tree. Some other fine Carabidae (*Iridagonum*, *Pogonoglossus*, etc.) occurred in the same place, and also scorpions, one of which stung me viciously on the finger as I was carrying down and washing out the mass of leaf-debris in the pools of a small brook.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. So far as I can find, this insect is not very closely related to anything previously known. In appearance it somewhat suggests *Dirotus subiridescens* Macl. or *extensicollis* (Bates), but its technical characters, including those of the tarsi, are very different (*e.g.* in *Dirotus* the elytra are fully margined at base and the tarsi are slender).

Genus EUPLENES S.-G.

Schmidt-Goebel 1846, Faun. Coleop. Birmaniae, p. 52.

Csiki 1931, Coleop. Cat., Carabidae, Harpalinae **5**, p. 767 (see for additional references).

Diagnosis. See key to genera, above.

Description. None required here.

Genotype. *E. cyanipennis* S.-G.

Generic distribution. Oriental Region to Japan, Philippines, New Guinea, Solomons; and Africa and Madagascar.

Notes. The Oriental species of this genus are very uniform in structure but differ among themselves strikingly in color and slightly in proportions, sculpture, etc.

Key to the Species of Euplenes of New Guinea

1. Elytra blue or greenish-blue, each with a conspicuous yellow blotch before middle, but with apices not rufescent (p. 122) .... *laetus*
– Elytra blue, without discal blotches, but with apices rufescent (p. 123) . . . *apicalis*

EUPLENES LAETUS n. sp.

Description. Form as usual in genus, broad, rather flat, *Lebia*-like; head, prothorax, lower surface, and appendages rufous; elytra blue or greenish-blue, slightly reddish in scutellar and anterior sutural area, and each with a conspicuous, elongate-oval, yellow blotch before middle centering on 5th interval but invading 4th and 6th ones; moderately shining; microsculpture faint on head but apparently isodiametric, a little more distinct and slightly transverse on pronotum, still more distinct and more transverse on elytra; head, pronotum, and elytral intervals with also very fine, sparse, inconspicuous punctulation. *Head* formed as usual in genus, .74 & .71 width prothorax. *Prothorax* broad; width/length 1.56 & 1.59; base/apex about 1.4, but anterior angles too broadly rounded for accurate measurement of apex; sides broadly rounded for much of length, then sinuate just before base; basal angles obtuse but nearly right, slightly blunted; basal foveae broad and shallow (as usual), they, basal area between them, and sides of pronotum moderately punctate. *Elytra* normal in genus, broad, with slight subapical sinuations of lateral margins before broadly rounded apices; striae moderately impressed, more or less distinctly punctulate; intervals slightly convex on disc, more so laterally; 5th interval broadly impressed at yellow blotch, the impression associated with some distortion of striae 3 to 6; 3rd interval with usual 3 discal punctures, anterior and middle ones by 3rd stria, posterior one nearer 2nd stria. *Inner wings* fully developed. *Lower surface, legs,* etc. normal for genus. *Measurements:* length 7.6–7.7; width 3.3–3.4 mm.

Types. Holotype ♂ (Leiden Mus.) from mountain slope above Bernhard Camp, Snow Mts., **Neth. N. G.**, 100 m. (about 325 ft.) altitude, Apr. 1939; and paratypes (M.C.Z. No. 28,590, and Buitenzorg Mus.) from the same general area (Snow Mts.) as follows: 1, Idenburg River, 400 m. (about 1,300 ft.), July 15–Nov. 15, 1938; and 3, Baliem Camp, 1,600 & 1,700 m. (about 5,200 & 5,525 ft.), Nov. & Dec. 1938 (all Toxopeus).

Other material. One specimen, not a type, from Malaita, **Solomon Islands** (American Mus.).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Baliem Camp.

Notes. This is very close to *Euplenes guttatus* Andr., which occurs from the Malay Peninsula to Celebes, but the elytra are primarily green in *guttatus*, blue in *laetus*. The latter may prove to be no more than a geographical subspecies of the former, but I do not like to use trinomials until the real relationships of the various forms are better understood than they yet are in this genus.

EUPLENES APICALIS n. sp.

Description. Form as usual in genus; head, prothorax, lower surface, and appendages red; elytra dark blue with apices red; surface moderately shining; microsculpture indistinct on head, faint and transverse on pronotum, more distinct (but still light) and more transverse on elytra; sparse punctulation of upper surface even finer than in *laetus*, scarcely visible at 54×. *Head* formed as usual in genus, .74 & .73 width prothorax. *Prothorax* broad; width/length 1.47 & 1.52; base/apex about 1.25 (apex cannot be measured accurately, for anterior angles indeterminate); sides moderately rounded (a little less so than in *laetus*), not or slightly sinuate before base, except basal angles minutely prominent; basal foveae broad and shallow, they and area between them and sides of pronotum before them moderately, irregularly punctate. *Elytra* normal in genus; striae moderately impressed, distinctly punctulate; intervals nearly flat or slightly convex on disc, more convex laterally; 5th interval with a strong longitudinal impression before middle accompanied by some distortion of striae 3 to 6; 3rd interval 3-punctate as in *laetus*. *Inner wings* fully developed. *Lower surface, legs*, etc. normal for genus. *Male copulatory organs* as figured (Fig. 22). *Measurements:* length 6.9–7.7; width 3.0–3.4 mm.

Types. Holotype ♂ (M.C.Z. No. 28,591) and 8 paratypes from Dobodura, **Papua**, Mar.–July 1944 (Darlington), in piles of dead leaves on the ground and clumps of dead leaves on fallen trees, in forest. Also additional paratypes as follows: **Papua**, 1, Milne Bay, Dec. 1943 (Darlington); 1, Fly River 5 miles below Palmer River, May 23–31, 1936 (Archbold Exp., American Mus.). **Neth. N. G.**: 1, Sabron, Cyclops Mts., 2,000 ft., July 1936 (Cheesman); 1, Cyclops Mts., 900 m. (about 2,925 ft.), end of June 1938 (Toxopeus); 2, Rattan Camp, Snow Mts., 1,200 m. (about 3,900 ft.), Feb.–Mar. 1939 (Toxopeus); and 1, Araucaria Camp, Snow Mts., 800 m. (about 2,600 ft.), Mar. 1939 (Toxopeus).

Other material. One badly damaged immature specimen from **Waigeo Island** (Cheesman); and 2 ♀♀ from Cape Gloucester, **New Britain** (Darlington).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Dobodura.

Notes. The coloration of this species is unique in the genus, so far as I know.

(Genus DICRANONCUS Chd.)

Chaudoir 1850, Bull. Soc. Nat. Moscow **23**, 2, p. 392.

Csiki 1931, Coleop. Cat., Carabidae, Harpalinae **5**, p. 742 (see for additional references).

Diagnosis. See key.

Description. None needed here.

Genotype. *D. femoralis* Chd.

Generic distribution. Oriental Region to Japan, the Philippines, the Solomons, and northeastern Australia; but not yet found in New Guinea.

(DICRANONCUS QUEENSLANDICUS (Sloane))

Platynus queenslandicus Sloane 1903, Proc. Linn. Soc. New South Wales **28**, pp. 632 (in key) & 633.

Dicranoncus queenslandicus Sloane 1920, *op. cit.* **45**, p. 322.

Description. The following description is for superficial recognition only. Rather slender, dark brown, about 7 mm. long; *head* rather small; *prothorax* suboval; *elytra* with sutural angles denticulate; all standard supraocular and lateral pronotal setae present; wings full; and tarsal claws of course toothed. *Male copulatory organs* illustrated in Fig. 23.

Type. From Mackay, Queensland, Australia; should now be in the Sloane Collection at Canberra, Australia.

Occurrence in New Guinea. Not yet recorded.

Notes. Although I have not seen this species from New Guinea, it probably occurs there or, if not, its absence is noteworthy, for it is now known from northeastern **Australia**, Guadalcanar Is. in the **Solomons** (J. A. Husche, Bishop Mus.), Cape Gloucester in western **New Britain** (Darlington), **Celebes** (received from C. J. Louwerens), **Sumbawa** (British Mus.), **Java** (received from Louwerens), the **Philippines**, and southern **India** and **Ceylon**. In Luzon I found it in clumps of tall grass in open country, not in shaded masses of vines and shrubbery frequented by *D. quadridens.* It should be looked for in the *kunai* grass in New Guinea.

Genus LOROSTEMMA Mots.

Motschulsky 1864, Bull. Soc. Nat. Moscow **37**, 4, p. 329 (*Lorostema*).
Csiki 1931, Coleop. Cat., Carabidae, Carabinae **5**, p. 875 (see for additional references).

Diagnosis. See key.

Description. I am not ready fully to describe or even to characterize this genus now. It includes some species which are rather striking in appearance, with long antennae, as well as some which are very *Agonum*-like, like the present one. They are all dull, often alutaceous, with elytral apices often (but perhaps not always) very finely more or less subserrate or granulate, and 4th hind-tarsal segment simply emarginate. I suspect, but have not yet confirmed my suspicions, that certain eastern Asiatic and Australian species now listed (in *Coleopterorum Catalogus*) under *Agonum* or *Anchomenus* will go into *Lorostemma* when the latter is properly defined.

Genotype. L. alutaceum Mots.

Generic distribution. The main part of the Oriental Region to Japan, the Philippines, and New Guinea and New Britain.

Notes. See discussion under description, above.

LOROSTEMMA INFORMALIS n. sp.

Description. *Agonum*- or *Notagonum*-like; dark-brown to piceous-black with faint aeneous lustre, lower surface and appendages slightly paler, outer margins of prothorax and elytra more or less paler and translucent; surface moderately shining, less alutaceous than usual in genus; microsculpture normal. *Head* .78 & .77; eyes large, prominent; both pairs supraocular setae present, posterior ones slightly before line of posterior edges of eyes; antennae not elongate (in genus), with 4th segment about 4× long as wide, scarcely longer than 3rd; neck only slightly, indefinitely impressed above; front normal. *Prothorax* subcordate; width/length 1.48 & 1.49; base/apex 1.16 & 1.22; sides moderately rounded, sometimes faintly angulate at anterior setae, moderately or scarcely sinuate before base; anterior angles not advanced beyond line of (broadly emarginate) anterior edge of pronotum; posterior angles obtuse but distinct and usually well formed; lateral margins moderately broad, moderately reflexed, each with a seta about ⅖ from apex and at base; basal foveae simple, rather poorly defined, moderately deep, strongly microreticulate, vaguely punctate; anterior marginal line entire, deep; posterior one obsolete; disc normal, impunctate except vaguely punctate at sides near foveae. *Elytra* of about outline and convexity of normal *Agonum s. s.* but with disc often faintly and irregularly impressed; basal margins entire, rounded or faintly subangulate at humeri; lateral margins moderate, rounded or vaguely subangulate before subapical sinuations; latter rather strong; apices independently more or less rounded, without or with only a suggestion of teeth at sutural angles; apical margin at least in part irregularly, finely subserrate or with projecting granules (these marginal details sometimes faint); striae rather deep, impunctate; intervals moderately convex, 8th a little narrowed and very convex toward apex, 9th wide and only slightly convex toward apex; 3rd interval normally 3-punctate, the punctures well impressed. *Inner wings* full. *Lower surface* impunctate or nearly so; abdomen not pubescent; prosternal process normal; mesepimera narrow; metepisterna moderately long. *Legs:* hind tibiae not or vaguely sulcate along outer edges (but middle tibiae are thus sulcate); hind tarsi with 4th segment simply emarginate, 5th segment without obvious accessory setae, sole with a nearly regular single row of strong setae each side of segments 1 to 4 but with middle of sole bare; claws simple. *Secondary sexual characters* normal. *Male copulatory organs* as figured (Fig. 24), with apex of middle lobe beyond orifice slightly compressed in vertical plane. *Measurements:* length 6.0–7.9; width 2.5–3.2 mm.

Types. Holotype ♂ (M.C.Z. No. 28,592) and 17 paratypes from Dobodura, **Papua**, Mar.–July 1944 (Darlington); and additional paratypes as follows: **Papua:** 26, Oro Bay (near Dobodura), Dec. 1943 (Darlington); 4, Lake Daviumbu, Fly River, Aug. 19–30, 1936 (Archbold Exp., American Mus.). **N-E. N. G.:** 1, Aitape, Aug. 1944 (Darlington). **Neth. N. G.:** 14, Hollandia, July–Sept. 1944 (Darlington); 4, Maffin Bay, Aug. 1944 (Darlington); 19, Sansapor (Vogelkop), Aug. 1944 (Darlington). My specimens taken in wet places, especially in swamps.

Other material. One specimen from Cape Gloucester, **New Britain**, Jan.–Feb. 1944 (Darlington).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Dobodura.

Notes. This is very much like *Lorostemma subnitens* Andr. of Sumatra, etc., but usually lacks the blunt denticles ("recurrent angles") at sutural angles of the elytra which are present in *subnitens* (I have a cotype of the latter before me); actually the denticles are more or less developed in a few specimens of *informalis,* though not in most. The New Guinean form may prove to be only a subspecies of *subnitens,* but I prefer to treat it as a species pending a better understanding of the interrelationships of the few known forms of the genus.

NOTAGONUM new genus

Diagnosis. Small or medium-sized (4.8 to 9.7 mm.), *Bembidion-* or *Agonum-* or *Platynus-*like forms; never brightly colored, rarely strongly iridescent; with fully developed wings and all usual supraocular and lateral pronotal setae and dorsal punctures of 3rd elytral intervals; and in general without unusual or striking characters; hind tarsi slender with 4th segment variable, 5th segment without obvious accessory setae. See also key to genera, above.

Description. Form as described above; color black, piceous, or reddish, with lateral margins of prothorax and elytra sometimes translucent or pale, and appendages in some cases dark, in others pale; surface often slightly but rarely strongly iridescent, moderately shining usually almost impunctate above except in some cases punctate in or in and between basal foveae of pronotum; microsculpture usually light, normal in many species, not so in others, as described. *Head* only moderately elongate in tribe; mandibles about normal in length and arcuation; eyes usually at least moderately large and prominent, with both pairs of supraocular setae present, the posterior ones usually between or very little behind level of posterior edges of eyes (but in *reversior* eyes are small but abruptly prominent, with posterior supraocular setae well behind level of their posterior edges, and eyes are reduced in an aberrant specimen of *sinuum* too); antennae moderately slender, normal in form, pubescent from near base of 4th segment (as usual); neck not or only slightly impressed above; front usually normal, with slight anterior impressions; mentum tooth triangular, somewhat variable, usually more or less blunted and sometimes even faintly emarginate at tip. *Prothorax* variable in form and proportions; anterior angles not or moderately advanced, posterior ones usually distinct, but variable; lateral margins variable in width, but always with usual 2 setae; basal foveae simple (as usual in tribe), reaching margins, usually moderately impressed, sometimes less impressed or flat; disc of pronotum normal; anterior and posterior marginal lines variable, as described in species. *Elytra* more or less normally *Agonum*-like in outline, varying somewhat in convexity, often impressed on disc; basal margin entire, rounded or very obtusely angulate at humeri (this character somewhat variable in single species), more distinctly angulate at humeri in *reversum* and *reversior*; lateral margins moderate or narrow; outer subapical angle usually rounded, but distinct in *externum*; subapical sinuations of margin strong, moderate, weak, or rarely absent; apices variable, rounded, denticulate, angulate, or rarely spined (if spined, spines about opposite ends of 3rd intervals); striae entire (as usual), variably impressed, usually not or not distinctly punctulate, but sometimes distinctly so; intervals varying in convexity in different species; 8th & 9th somewhat variable toward apex but never deeply longitudinally impressed; no 10th interval indicated; 3rd interval always normally 3-punctate. *Inner wings* always fully developed; metepisterna moderately long. *Lower surface* usually impunctate or nearly so, usually not pubescent, but with slight or extensive pubescence on abdomen in a few species; prosternal process normal, not margined, without setae; mesepimera narrow. *Legs* normally formed; hind tibiae not sulcate along outer edges; hind tarsi slender, more or less sulcate on both sides above at least basally (the sulci vary somewhat in different species but are difficult to see and interpret); 4th hind-tarsal segment variable, simply emarginate or with short, medium, or long lobes, with outer lobe longer than inner; 5th hind-tarsal segment without obvious accessory setae but sometimes (perhaps always) with minute rudiments or vestiges of them; claws simple; sole of hind tarsus usually clothed with rather sparse, scattered bristles, with middle of sole not or only narrowly bare (but in *subrufum* the bristles form a nearly regular row on each side, and middle of sole is more broadly bare). *Secondary sexual characters* normal, except in *altum* ♀ has usually only 1 (not 2) seta each side last ventral segment. *Male copulatory organs* as figured for certain species (Figs. 25–33), fairly constant in general structure but varying in some details, especially form of apex of middle lobe and armament of internal sac.

Genotype. *Notagonum externum* n. sp. (below).

Generic distribution. Numerous in New Guinea; some species elsewhere in the Indo-Australian Archipelago; further distribution not determined.

Notes. Many of the species of this genus, including the genotype, are superficially similar to some northern *Agonum*, but differ by absence of obvious accessory setae on the 5th tarsal segments and by absence of certain other setae of the legs. Most (but not all) of the species would be included in *Colpodes* in a conventionally broad sense because the 4th hind-tarsal segment is more or less lobed, but, as I have said, this character varies from species to species and is not worth the stress it has received in the past. It must be admitted that it is hard to draw a line between *Colpodes* in my partly restricted sense and some of the forms which I am including in *Notagonum*, but I am convinced that when *Colpodes* is broken up the various species of *Notagonum* will properly form at least one and perhaps more separate genera.

All the species of *Notagonum* that I have collected are ground-living, not arboreal, and none is found in very dry open places. With these limitations, they occur in a variety of habitats. Several, especially the more slender, large-headed forms (*angustellum*, etc.), live by running water, but each shows a definite preference for a particular type of stream, large or small, shaded or unshaded, etc. A number of species, including those that most resemble typical *Agonum*, inhabit various other wet places. *N. paludum* occurs with certain Oodiini among very wet dead leaves at the edges of pools in forest. And *N. spinulum* I found only among dead leaves on the ground in heavy rainforest, with the very similar and perhaps actually related *Altagonum vallicola*. Most of the species of *Notagonum* inhabit lowlands or foothill areas, but a few of the lowland forms occur also in the mountains, and a few species are apparently confined to rather high altitudes.

The following three species, described from New Guinea many years ago by Maindron, are probably referable to *Notagonum*, but the descriptions are inadequate for even tentative identification.

Previously described species probably referable to Notagonum, but not identifiable from description

Colpodes albertisi Maindron

Maindron 1906, Bull. Soc. Ent. France, p. 24.
—— 1908, *Op. cit.*, p. 186.

Types. From the Fly River; probably in the Paris Museum.

Colpodes laglaizei Maindron

Maindron 1908, Nova Guinea **5**, p. 297.

Type. From Timena (probably the Timena River, south of Lake Sentani, Neth. N. G.); probably in the Paris Museum.

Colpodes novae-guineae Maindron

Maindron 1908, Nova Guinea **5**, p. 296.

Type. From Jamur Superieur (probably region of Lake Jamur, Neth. N. G.); probably in the Paris Museum.

These species are not included in the following key.

Key to the Species of Notagonum of New Guinea

1. Head relatively wide, .85 to .95 width prothorax; (in border-line cases refer here specimens with ventral pubescence, or with sides of prothorax sinuate ¼ or more of length before base) 2

— Head relatively narrower, .63 to .84 width prothorax; (if ventral pubescence present, head obviously less than .84 width prothorax; sides of prothorax never sinuate so far forward) 6

2. Sides of prothorax sinuate relatively near base; at least part of ventral surface of abdomen pubescent 3

— Sides of prothorax sinuate ¼ or ⅓ of length before base; abdomen not pubescent, except for fixed setae 5

3. Much of abdomen including most of last segment pubescent; (small, slender, depressed, with very long antennae) (p. 133) . . . . . . *angustellum*

— Abdomen much less extensively pubescent 4

4. Depressed; black, legs blackish; lateral margins of prothorax narrower, not distinctly translucent (p. 134) . . . . *subnigrum*

— Less depressed; brownish-piceous, legs yellow or brown, rarely blackish; lateral margins of prothorax wider (but still rather narrow), more or less translucent (p. 135) . . . . *vile*

5. Eyes normal, with posterior supraocular setae about between their posterior margins; prothorax wider than long, not punctate across base (p. 136) . . . . *reversum*

— Eyes smaller but abruptly prominent, with posterior supraocular setae well behind line of their posterior margins; prothorax as long as wide (by measurement), extensively punctate across base (p. 137) . . *reversior*

6. Apices of elytra at least in part very finely subserrate or granulate, though sometimes only faintly so (piceous, *Agonum*-like, with 4th hind-tarsal segment simply emarginate) (inserted here because of similarity to some *Notagonum*) (p. 126) . . . . (*Lorostemma informalis*)

— Apices of elytra not subserrate or granulate (form, appearance, and form of 4th hind-tarsal segment variable) 7

7. Lateral margin of elytron with an abrupt, sharply defined angle before the subapical sinuation (p. 138) . . . . *externum*
— Lateral margin of elytron not abruptly angulate before the subapical sinuation 8
8. Apex of each elytron more or less rounded, not distinctly denticulate, not abruptly angulate, not spined 9
— Apex of each elytron denticulate at suture, and/or abruptly angulate or spined about opposite 3rd interval 14
9. Abdomen extensively pubescent; 9th (submarginal) interval of elytron near apex rather narrow and strongly convex 10
— Abdomen not pubescent, except for fixed setae; 9th interval of elytron near apex wider and nearly flat 11
10. Sides of prothorax strongly sinuate, with posterior angles right or nearly so; basal foveae of pronotum shallow, almost flat, much roughened (p. 139) . . . . *sinuum*
— Sides of prothorax only moderately sinuate, with posterior angles a little obtuse; basal foveae of pronotum rather deep, less roughened (p. 140) *vaporum*
11. Small (4.8–6.5 mm.) lowland species; 4th hind-tarsal segment simply emarginate . . . . *aitape*
    (11a) Elytron with pale margin confined to lateral gutter; average size smaller (4.8–5.6 mm.) (p. 141) . . . . (*aitape* s. s.)
    (11b) Elytron with pale margin including several outer intervals; average size larger (5.5–6.5 mm.) (p. 142) . . . . (subsp. *sansapor*)
— Larger (7.1–8.6 mm.) mountain species; 4th hind-tarsal segment lobed . . 12
12. Form very convex, the pronotum gibbous and with exceptionally narrow margins; (elytra lightly striate, inner striae often almost obliterated anteriorly) (p. 142) . . . . *gibbum*
— Form less convex, the pronotum only normally convex and with margins only normally narrow 13
13. Elytra more than usually narrowed toward base, deeply striate; microsculpture of elytra coarser, the meshes distinct at 54X . . . . *altum*
    (13a) Base of prothorax relatively wider (base/apex 1.15 to 1.22) (p. 144) (*altum* s. s.)
    (13b) Base of prothorax relatively narrower (base/apex 1.03 to 1.13) (p. 145) . . . . (subsp. *ibele*)
— Elytra not unusually narrowed basally, lightly striate; microsculpture of elytra very fine, the meshes not visible at 54X (p. 143) . . . . *sigi*
14. Apex of each elytron with a denticle at sutural angle but with no other denticle, no well-defined angulation, no spine 15
— Apex of elytron with a second denticle, or with a well-defined angulation or spine about opposite end of 3rd interval 18
15. Subapical sinuation of elytral margin rather weak; (elytral striae usually distinctly punctulate) (see also Couplet 20) (p. 145) . . . . *margaritum*
— Subapical sinuation of elytral margin strong; (elytral striae not distinctly punctulate 16
16. Basal foveae of pronotum irregularly punctate; 4th hind-tarsal segment simply emarginate . . . . *subpunctum*

(16a) Smaller (6.5–7.4 mm.); elytral microsculpture coarser, the meshes very distinct at 54X (p. 146) . . . . (*subpunctum s. s.*)

(16b) Larger (7.7–8.5 mm.); elytral microsculpture finer, the meshes barely visible at 54X (p. 147) . . . . (subsp. *capitis*)

— Basal foveae of pronotum not or indistinctly punctate; 4th hind-tarsal segment lobed 17

17. Elytra not distinctly impressed before middle, their outer margins contrastingly pale . . . . *dentellum*

(17a) Smaller (7.3–8.5 mm.); eyes relatively larger and more prominent; etc. (see description) (p. 147) . . . . (*dentellum* s. s.)

(17b) Larger (8.4–9.7 mm.); eyes relatively smaller and less prominent; etc. (see description) (p. 149) . . . . (subsp. *chimbu*)

— Elytra broadly impressed across disc ⅓ or ⅖ from base, their outer margins not contrastingly pale (p. 149) . . . . *subimpressum*

18. Apex of each elytron bi-denticulate or bi-angulate, the outer denticle or angle (about opposite end of 3rd interval) only about as prominent as the inner (sutural) one 19

— Apex of each elytron strongly angulate or spined about opposite 3rd interval, the angulation or spine much more prominent than the sutural denticle, if any 22

19. Small (5.6–6.6 mm.); elytra not distinctly iridescent . . . . *paludum*

(19a) Microsculpture of elytra coarser, the meshes very distinct at 54X (p. 150) . . . . (*paludum s. s.*)

(19b) Microsculpture of elytra finer, the meshes barely or not visible at 54X (p. 151) . . . . (subsp. *velum*)

— Larger (7.0–9.0 mm.); elytra more or less iridescent 20

20. Legs yellowish; elytral striae usually punctulate; (see Couplet 15) . . . . *margaritum* in part

— Legs dark; elytral striae not distinctly punctulate 21

21. Slightly broader, with prothorax wider (slightly more than ½ wider than long) and head relatively narrower (.68 width prothorax), but with very prominent eyes; front of prothorax only normally emarginate (p. 151) *malkini*

— Slightly less broad, with prothorax narrower (slightly less than ½ wider than long) and head relatively wider (.71 to .74 width prothorax), though with less prominent eyes; front of prothorax more deeply emarginate (with anterior angles more advanced) than usual (p. 152) . . . . . . *iridior*

22. Elytra strongly angulate at apex opposite ends of 3rd intervals, but not spined 23

— Elytra spined at apex about opposite ends of 3rd intervals. 25

23. Broad, relatively small-headed (head/prothorax .66 & .69); lateral margins of prothorax scarcely translucent (p. 153) . . . . *addendum*

— More slender, relatively larger-headed (head/prothorax .77 to .80); lateral margins of prothorax contrastingly translucent 24

24. Prothorax narrower (width/length 1.30 in specimens measured) and with narrower base (base/apex 1.18 & 1.23 in specimens measured); elytra strongly iridescent (p. 154) . . . . *angulum*

— Prothorax wider (width/length 1.41 & 1.42) and with wider base (base/apex 1.33 & 1.36); elytra only faintly iridescent (p. 155) . . . . *subangulum*
25. Broad, black, lowland species 26
— Slender, rufescent, mountain species (p. 156) . . . . *subrufum*
26. Larger (7.3–8.4 mm.); elytral striae lightly impressed; 4th hind-tarsal segment with very short lobes (p. 157) . . . . *spinulum*
— Smaller (6.8 mm.); elytral striae deeply impressed; 4th hind-tarsal segment without distinct lobes; (see also description) (p. 158) . . . . *subspinulum*

NOTAGONUM ANGUSTELLUM n. sp.

Description. With characters of genus as described above. Form of large, slender, flattened *Bembidion*; brownish-piceous above, scarcely paler below, appendages testaceous or brownish-testaceous, outer margins of prothorax and elytra only slightly translucent; surface moderately shining, not or faintly iridescent; microsculpture normal, light. *Head* .89 & .86 width prothorax; eyes large, prominent, with posterior supraocular setae just behind line of their posterior edges. *Prothorax* subcordate; width/length 1.34 & 1.40; base/apex 1.12 & 1.16; sides less arcuate than usual, sometimes faintly angulate at anterior marginal setae, rather broadly sinuate before basal angles; latter approximately right, well defined; lateral margins rather narrow; basal foveae flat, very shallow (but sometimes a little impressed), with surface somewhat irregular but not distinctly punctate; anterior marginal line faint or interrupted at middle, posterior one vague. *Elytra* rather narrow, subparallel, depressed; subapical sinuations moderate; apices more or less independently rounded, often vaguely angulate at suture, and rarely subdenticulate there; striae moderately deep, impunctate or faintly punctulate; intervals slightly convex, 8th narrowed and strongly convex apically, 9th wide apically, partly or completely interrupted by ocellate punctures, but remaining portions convex. *Lower surface* with at most a few vague punctures, except that abdomen, including nearly the whole of its last segment, has extensive pubescence rising from fine punctures. *Legs:* 4th hind-tarsal segment lobed, outer lobe longer than inner. *Male copulatory organs:* Fig. 25. *Measurements:* length 5.8–7.4; width 2.0–2.7 mm.

Types. Holotype ♂ (M.C.Z. No. 28,593), and 16 paratypes from Dobodura, **Papua**, Mar.–July 1944 (Darlington). Additional paratypes as follows: **Papua:** 7, Milne Bay, Dec. 1943 (Darlington), and 1, same locality, Oct. 20, 1943 (W. B. Jones, Alabama Mus. Nat. Hist.). **N-E. N. G.:** 14, Nadzab, July 1944 (Darlington); 16, Chimbu Valley, Bismarck Range, 5,000–7,000 ft., Oct. 1944 (Darlington). **Neth. N. G.:** 33, vicinity of Hollandia (actually S. foothills of Cyclops

Mts.), July–Sept. 1944 (Darlington); 1, Mt. Lina, Cyclops Mts., 3,500 ft., Mar. 1936 (Cheesman); 1, Mt. Cyclops, 3,500 ft., Mar. 1936 (Cheesman); 4, Sigi Camp, Snow Mts., 1,500 m. (about 4,875 ft.), Feb. 1939 (Toxopeus); 1, Rattan Camp, Snow Mts., 1,150 m. (about 3,750 ft.), Feb.–Mar. 1939 (Toxopeus).

Other material. Six specimens from Sigi Camp, Snow Mts., 1,500 m. (about 4,875 ft.), Feb. 1939 (Toxopeus); and 2, Araucaria Camp, Snow Mts., 800 m. (about 2,600 ft.), Mar. 1939 (Toxopeus). These specimens have the ventral pubescence of *angustellum* but approach *subnigrum* (below) in color and (especially the Araucaria Camp specimens) in appearance. I should consider them a subspecies of *angustellum* except that more typical specimens of the latter occur in the Snow Mts., including Sigi Camp, too.

Measured specimens. The ♂ holotype and 1 ♀ paratype from Dobodura.

Notes. This species is easily recognized by its small size, slender and depressed form, long antennae, and extensively pubescent abdomen. The last character is repeated in *Notagonum sinuum* and *vaporum* which, however, are differently shaped, much wider species, with relatively narrower heads. Specimens of *angustellum* from different localities vary a little in size and appearance, but I cannot define recognizable subspecies. My specimens were all taken among stones by rapid streams. At Dobodura, *angustellum* occurred only beside small streams in forest. Along larger, opener streams it was replaced by *Notagonum subnigrum* and *Lithagonum annulicorne,* which also live among stones or in stone-and-gravel bars.

NOTAGONUM SUBNIGRUM n. sp.

Description. With characters of genus as described above. Form of a very large, slender, slightly flattened *Bembidion*; black or piceous above and below, legs and first 4 antennal segments blackish, outer antennal segments browner, lateral margins of prothorax and elytra not translucent; surface moderately shining, not iridescent; microsculpture normal. *Head* .90 & .88 width prothorax; eyes large, prominent, with posterior supraocular setae about between their posterior margins. *Prothorax* quadrate-subcordate; width/length 1.36 & 1.41; base/apex 1.10 & 1.15; sides less arcuate than usual, strongly sinuate about 1/6 or 1/7 of length before basal angles; latter approximately right, very well defined; lateral margins narrow; basal foveae very shallow, flat, with surface somewhat irregular but not distinctly punctate; anterior marginal line widely interrupted at middle, posterior one vague. *Elytra* rather narrow but with sides a little more arcuate than in *angustellum,* subdepressed; lateral margins narrow; subapical sinuations moderate; apices independently more or less rounded to suture, not denticulate; striae moderately impressed, the outer ones especially more or less distinctly punctulate; intervals nearly flat or slightly convex, 8th and 9th not much modified toward apex. *Lower surface* nearly impunctate except that abdomen has a little scattered pubescence (much less than in *angustellum*) rising from fine punctures. *Legs:* 4th hind-tarsal segment lobed, outer lobe longer than inner. *Measurements:* length 7.5–8.3; width 2.8–3.1 mm.

Types. Holotype ♂ (M.C.Z. No. 28,594) and 28 paratypes from Dobodura, **Papua**, Mar.–July 1944 (Darlington); and 1 ♂ paratype from Kokoda, **Papua**, 1,200 ft., Sept. 1933 (Cheesman). My specimens were taken in cobble-stone-and-gravel bars and in other cover by fairly large streams.

Measured specimens. The ♂ holotype and 1 ♀ paratype from Dobodura.

Notes. This is sufficiently distinguished from other species in the key, above. There is no sign of intergradation between this species and *angustellum* at Dobodura, but some specimens of *angustellum* from the Snow Mts. of Netherlands New Guinea are somewhat *subnigrum*-like at least superficially, as already noted.

NOTAGONUM VILE n. sp.

Description. With characters of genus as described above. Form of a very large *Bembidion* (*Peryphus*) or small *Agonum* (*Europhilus*); brownish-piceous, legs yellowish or brownish, antennae brownish, outer margins of prothorax and elytra somewhat paler or translucent; surface moderately shining, not or faintly iridescent; microsculpture normal, light. *Head* .86 & .89 width prothorax; eyes large, prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* more or less subcordate; width/length 1.35 & 1.35; base/apex 1.26 & 1.23; sides moderately arcuate, then moderately sinuate a little before posterior angles; latter right or slightly obtuse, very little blunted; lateral margins rather narrow; basal foveae somewhat variable, flat to moderately impressed, roughened but not punctate; anterior marginal line variable, light or interrupted at middle, posterior one vague. *Elytra* slightly shorter than in preceding species, of about average outline and convexity, with disc sometimes faintly impresse- before middle; lateral margins normal; subapical sinuations moderated apices independently more or less rounded to suture, rarely sub; denticulate at sutural angles; striae moderately impressed, not or faintly punctulate; intervals flat or slightly convex, 8th and 9th not much modified toward apex. *Lower surface* nearly impunctate, but abdomen with a little scattered pubescence (much less than in *angustellum*) chiefly along median area. *Legs:* 4th hind-tarsal segment lobed, outer lobe longer than inner. *Measurements:* length 6.7–8.2; width 2.7–3.3 mm.

Types. Holotype ♂ (M.C.Z. No. 28,595) and 26 paratypes from Dobodura, **Papua**, Mar.–July 1944 (Darlington); and 4 paratypes from Oro Bay (near Dobodura), Dec. 1943–Jan. 1944 (Darlington).

Other material. **Papua:** 9, Milne Bay, Dec. 1943 (Darlington), and 1, same locality, Oct. 20, 1943 (W. B. Jones, Alabama Mus. Nat. Hist.); 3, Palmer River at Black River, June & July 1936 (Archbold Exped., American Mus.). **N-E. N. G.:** 17, Lae, Oct. 1944 (Darlington); 15, Nadzab, July 1944 (Darlington); 9, Surprise Creek, Morobe Dist., Sept. & Oct. (Stevens, M.C.Z.); 62, Chimbu Valley, Bismarck Range, 5,000–7,500 ft., Oct. 1944 (Darlington). **Neth. N. G.:** 31, vicinity of Hollandia (actually S. foothills of Cyclops Mts.), July–Sept. 1944 (Darlington); 1, Cyclops Mts., 3,500 ft., Mar. 1936 (Cheesman), and 1 Cyclops Mts. without further locality (Cheesman); 2, Bewani Mts., Humboldt Bay Dist., 400 m. (about 1,300 fet.), July 1937 (W. Stüber, British Mus.); 6, Araucaria Camp, Snow Mts., 800 m. (about 2,600 ft.), Mar. 1939 (Toxopeus); 2, Sigi Camp, Snow Mts., 1,500 m. (about 4,875 ft.), Feb. 19 & 25, 1939 (Toxopeus); 2, Sansapor (Vogelkop), Aug. 1944 (Darlington). Also **New Britain:** 28, Cape Gloucester, Jan.–Feb. 1943 (Darlington).

Measured specimens. Holotype ♂ and 1 ♀ paratype from Dobodura.

Notes. See key (above) for distinguishing characters of the species. It is very common, in my experience, in grass and other cover beside large streams in more or less open country. The species varies both individually and geographically. I cannot now define useful subspecies, but it is likely that they will be recognized in the future. In the meantime, and for this reason, I have limited the actual type series to specimens from a restricted area.

NOTAGONUM REVERSUM n. sp.

Description. With characters of genus as described above. Form of preceding (*vile*) but a little more slender and convex; piceous-black, lower surface, legs, and antennal bases brownish-piceous, lateral margins of prothorax and elytra not noticeably paler; surface moderately shining, not distinctly iridescent; microsculpture normal, light. *Head* .87 & .85 width prothorax; eyes moderately large and prominent, with posterior supraocular setae about between their posterior margins.

Prothorax quadrate-subcordate, wider than long; width/length 1.18 & 1.18; base/apex 1.25 & 1.23; sides moderately arcuate anteriorly, strongly sinuate ¼ or more of length before base; posterior angles more or less acute, very well defined; lateral margins narrow; basal foveae shallow, flat or vaguely linear, not punctate and not much roughened; anterior marginal line more or less interrupted at middle, posterior one usually lightly impressed. *Elytra* rather elongate and convex; marginal line distinctly but obtusely angulate at humeri; lateral margins rather narrow; subapical sinuations rather weak; apices irregularly almost conjointly rounded, slightly produced, vaguely angulate (not denticulate) near sutural angles; striae moderately impressed, more or less punctulate; intervals moderately convex, 8th and 9th not much modified toward apex. *Lower surface* not distinctly punctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment lobed, outer lobe longer than inner. *Measurements:* length 7.3–8.6; width 2.7–3.3 mm.

Types. Holotype ♂ (M.C.Z. No. 28,596) and 11 paratypes all from Chimbu Valley, Bismarck Range, **N-E. N. G.**, 5,000–7,500 ft., Oct. 1944 (Darlington), taken along streams in open country.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This species is distinguished from all others of the genus except the following (*reversior*, *q.v.*) by the form of the prothorax, with sides sinuate at least ¼ of the prothoracic length before the base.

NOTAGONUM REVERSIOR n. sp.

Description. With characters of genus as described above, except eyes abnormal (see below). Form of preceding (*reversum*), rather slender and convex; brownish-piceous, slightly paler below, legs and antennae brownish-yellow, lateral margins of prothorax and elytra not distinctly paler; surface moderately shining, not iridescent; microsculpture normal but light and restricted. *Head* .93 & .95 width prothorax; eyes relatively small but abruptly prominent, with posterior supraocular setae well behind line of their posterior edges. *Prothorax* subquadrate, relatively narrow anteriorly; width/length 1.00 & .99; base/apex 1.44 & 1.35; sides slightly, more or less irregularly arcuate anteriorly, rather strongly sinuate about ⅓ of length before base; basal angles acute; lateral margins very narrow; basal foveae only moderately impressed but entire basal area strongly depressed in the type and paratype but not in the third specimen; entire base of prothorax irregularly punctate in all specimens; anterior marginal line entire or nearly so, posterior one entire. *Elytra* suboval in the type and paratype, longer in the third specimen; broadly and irregularly impressed about ⅓ from base; marginal line moderately angulate at humeri; outer margins rather narrow; subapical sinuations absent; apices rather narrowly rounded, not denticulate in the type and paratype but strongly denticulate (at sutural angles) in the third specimen; striae moderately impressed, faintly or not punctulate; intervals slightly convex, 8th and 9th not much modified toward apex. *Lower surface* with sides of sterna more or less punctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment lobed, outer lobe longer than inner. *Male copulatory organs:* Fig. 26. *Measurements:* length 8.6; width 3.3 mm. (third specimen 9.3 by 3.4 mm.).

Types. Holotype ♂ (Leiden Mus.) and 1 ♀ paratype (M.C.Z. No. 28,597) from Moss Forest Camp, Snow Mts., **Neth. N. G.**, 2,800 m. (about 9,100 ft.), Oct. 9–Nov. 5, 1938 (Toxopeus).

Other material. A third specimen with the same data as the types, but differing from them in several rather striking details.

Measured specimens. The ♂ ♀ types.

Notes. This species is probably related to *reversum* (above), but differs from it in several characters including form of eyes, which are unique in *Notagonum.* However, more or less similar "popped" eyes occur in several other, unrelated groups of Agonini, as already noted in the introduction. The differences in form of base of prothorax and in form and apices of elytra between the types and the third specimen mentioned above are so great that I should consider the third specimen a different species, if it came from a different locality. However, since all the specimens are from one locality, I think it likely that they all represent one strikingly dimorphic species.

NOTAGONUM EXTERNUM n. sp.

Description. With characters of genus as described above. Form of *Agonum s. s.* (Fig. 2); piceous-black, lower surface only slightly paler, antennae and legs more or less dark-brown, lateral margins of prothorax and elytra more or less pale-translucent; surface moderately shining, not iridescent; microsculpture normal. *Head* .81 & .76 width prothorax (head still narrower in some specimens); eyes large, prominent, with posterior supraocular setae between their posterior edges. *Prothorax* subcordate; width/length 1.47 & 1.49; base/apex 1.30 & 1.25; sides normally arcuate, moderately or slightly sinuate before posterior angles; latter obtuse or nearly right, blunted or narrowly rounded; lateral margins moderate; basal foveae deep, not sharply defined, micro-reticulate but not punctate; anterior marginal line faint or interrupted at middle, posterior one faint. *Elytra* of normal outline and convexity; disc vaguely, broadly impressed about ⅓ from base; external margins moderate, each ending in a right or obtuse, well defined angle at the end of the lateral gutter; apices broadly emarginate from outer angle to opposite 3rd interval, then truncate to sutural angles; latter denticulate; striae deep, impunctate; intervals moderately convex, 8th and 9th not much modified toward apex. *Lower surface* almost impunctate; abdomen usually with a very little fine pubescence near middle. *Legs:* 4th hind-tarsal segment with a moderate outer and shorter inner lobe (Fig. 18). *Male copulatory organs* as figured (Fig. 27). *Measurements:* length 6.2–7.0; width 2.4–2.8 mm.

Types. Holotype ♂ (M.C.Z. No. 28,598) and 30 paratypes from Dobodura, **Papua**, Mar.–July 1944 (Darlington).

Other material. **Papua:** 23, Milne Bay, Dec. 1943 (Darlington); 1, Port Moresby, Oct. 1944 (Darlington). **Neth. N. G.:** 6, Sansapor, on Vogelkop, Aug. 1944 (Darlington).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This species is distinguished from all other members of the genus by the well-formed outer angles of the elytra. It apparently ranges over the whole of New Guinea, but I cannot divide it into subspecies. I know that the species occurs on the ground in wet places, but since I did not distinguish it in the field, I cannot define its habitat more exactly.

NOTAGONUM SINUUM n. sp.

Description. With characters of genus as described above. Form of *Agonum* (*Platynus*); piceous, legs and basal segments of antennae brownish-piceous, outer antennal segments paler brown, lateral margin of prothorax moderately translucent, of elytra scarcely so; surface moderately shining, not distinctly iridescent; microsculpture normal but less transverse than usual on elytra. *Head* .80 & .78 width prothorax; eyes moderately large and prominent, with posterior supraocular setae about between their posterior edges (but see aberrant specimen described below). *Prothorax* subcordate; width/length 1.38 & 1.41; base/apex 1.24 & 1.14; sides rather strongly arcuate anteriorly, strongly sinuate about 1/6 of length before base; posterior angles right or slightly obtuse, well defined; lateral margins moderate; basal foveae shallow, almost flat, much roughened, almost punctate; anterior marginal line more or less interrupted at middle, basal one vague or absent. *Elytra* of average outline and convexity; lateral margins normal; subapical sinuations moderate; apices more or less conjointly rounded, not distinctly denticulate; striae rather deep, not or faintly punctulate; intervals convex, 8th moderately narrowed toward apex

9th toward apex less wide and much more convex than usual. *Lower surface* at sides more or less subrugose or subpunctate; abdomen extensively pubescent. *Legs:* 4th hind-tarsal segment strongly lobed, outer lobe longer than inner. *Measurements:* length 6.6–7.5; width 2.5–3.0 mm.

Types. Holotype ♂ (M.C.Z. No. 28,599) and 7 paratypes from Chimbu Valley, Bismarck Range, **N-E. N. G.**, 5,000–7,500 ft., Oct. 1944 (Darlington). Additional paratypes from **Neth. N. G.:** 2, Mt. Cyclops, 3,500 ft., Mar. 1936 (Cheesman); 2, Araucaria Camp, Snow Mts., 800 m. (about 2,600 ft.), Mar. 1939 (Toxopeus).

Other material. One ♀, Sigi Camp, Snow Mts., 1,500 m. (about 4,875 ft.), Feb. 19, 1939 (Toxopeus). In this specimen the eyes, though of nearly normal shape, are reduced in size, so that the posterior supraocular setae are behind the line of their posterior edges. In all other characters (form, etc., sinuation of sides of prothorax, form of 9th elytral interval, pubescence of abdomen, form of 4th hind-tarsal segment, and form of mentum tooth, which is more or less emarginate at tip in this species) this specimen appears to be *sinuum*, of which I tentatively consider it a variant.

Measured specimens. The ♂ holotype and 1 ♀ paratype from Chimbu Valley.

Notes. The extensive abdominal pubescence, plus the general form and strong sinuation of the sides of the prothorax and also the unusual convexity of the 9th elytral interval toward apex, make this an easily recognized and strongly characterized species. It is probably closely related only to the following (*vaporum*), *q.v.*

NOTAGONUM VAPORUM n. sp.

Description. With characters of genus as described above. Form of *Agonum* (*Platynus*); piceous, legs and especially antennae browner, outer margins of prothorax moderately translucent, of elytra less so; surface moderately shining; microsculpture normal but less transverse than usual on elytra. *Head* .81 & .81 width prothorax; eyes moderately large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* subcordate; width/length 1.41 & 1.42; base/apex 1.17 & 1.15; sides irregularly arcuate anteriorly, moderately sinuate near base; basal angles a little obtuse (nearly right), well defined; lateral margins rather wide, a little reflexed and elevated toward base; basal foveae deep, moderately roughened; anterior marginal line more or less interrupted at middle, posterior one vague at middle. *Elytra* of average outline and convexity; disc vaguely impressed about basal ⅓; lateral margins normal; subapical sinuations rather slight;

apices irregularly rounded, vaguely angulate (not denticulate) near suture; striae rather deep, not or faintly punctulate; intervals slightly convex, 8th moderately narrowed toward apex, 9th unusually narrow and convex toward apex. *Lower surface* nearly impunctate; abdomen extensively pubescent. *Legs:* 4th hind-tarsal segment lobed, outer lobe longer than inner. *Male copulatory organs:* Fig. 28. *Measurements* length 6.5; width 2.5 mm.

Types. Holotype ♂ (Leiden Mus.) and 1 ♀ paratype (M.C.Z. No. 28,600) from Mist Camp, Snow Mts., **Neth. N. G.**, 1,800 m. (about 5,850 ft.), Jan. 1939 (Toxopeus).

Measured specimens. The types.

Notes. The general form, relatively narrow and convex apical part of the 9th (submarginal) elytral intervals, pubescent abdomen, and other details indicate that this species is closely related to the preceding (*sinuum*), but the prothorax of the present species is much less sinuate at sides, with wider and posteriorly much more elevated lateral margins and much deeper basal foveae.

NOTAGONUM AITAPE n. sp.

Description. With characters of genus as described above. Form of broad but very small *Agonum s. s.*; piceous, legs and antennae dark-brown, lateral margins of prothorax and elytra more or less conspicuously yellow; surface moderately shining, slightly iridescent especially on elytra; microsculpture nearly normal, but very fine (scarcely visible at 54×) on elytra. *Head* .70 & .71 width prothorax; eyes large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* rather large; width/length 1.52 & 1.55; base/apex 1.26 & 1.17; sides arcuate for most of length, slightly sinuate near base; basal angles obtuse and slightly blunted; lateral margins rather wide but only slightly reflexed; basal foveae not very deep, a little roughened but not punctate; anterior marginal line vague at middle, posterior one indistinct. *Elytra* of about normal outline and convexity; lateral margins rather wide (in group); subapical sinuations rather slight; apices rather irregularly independently rounded, more or less subangulate (not denticulate) near suture striae deep, not distinctly punctate; intervals more or less convex, 8th and 9th not much modified toward apex. *Lower surface* impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment emarginate at apex, not lobed. *Measurements:* length 4.8–5.6; width 2.0–2.4 mm.

Types. Holotype ♂ (M.C.Z. No. 28,601) and 10 paratypes all from Aitape, **N-E. N. G.**, Aug. 1944 (Darlington), taken in floodwater in forested or recently forested country.

Other material. One, vicinity of Hollandia, **Neth. N. G.**, July–Sept. 1944 (Darlington).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Aitape.

Notes. This species should be easily recognized by its small size, rather broad form, simple elytral apices, yellow lateral margins, and simply emarginate 4th hind-tarsal segment.

NOTAGONUM AITAPE SANSAPOR n. subsp.

Description. Apparently same as typical *aitape* (of which see description, above) in structure, but a little larger, and differing in color, the elytra having *broad* yellowish-brown lateral margins and the legs and antennae being paler. The pale elytral margins reach inwardly about to the 6th intervals, but are not sharply limited, grading into the piceous color of the elytral disc. Proportions: head/prothorax .71 & .70; width/length of prothorax 1.45 & 1.50; base/apex of prothorax 1.18 & 1.22. *Measurements:* length 5.5–6.5; width 2.2–2.7 mm.

Types. Holotype ♂ (M.C.Z. No. 28,602) and 21 paratypes all from Sansapor (Vogelkop), **Neth. N. G.**, Aug. 1944 (Darlington), taken in wet places on the ground in forested country.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. Sufficiently compared with typical *aitape* above.

NOTAGONUM GIBBUM n. sp.

Description. With characters of genus as described above. Form of a very large *Mecyclothorax* (much more convex than normal *Agonum*); piceous-black, elytra faintly brassy in some lights, appendages reddish-yellow, outer antennal segments browner, outer margins of prothorax and elytra slightly or not paler; surface shining, not or only faintly iridescent; microsculpture finer than usual, not distinct at 54×, but surface especially of elytra with silky texture. *Head* .78 & .77 width prothorax; eyes moderately large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* transverse-rounded, much more convex than usual; width/length 1.47 & 1.52; base/apex 1.13 & 1.17; sides arcuate for most of length, not or only slightly sinuate before basal angles; latter obtuse, blunted; lateral margins usually very narrow, but somewhat variable; basal foveae rather small, shallow, not well defined, somewhat roughened or vaguely punctate; anterior and posterior marginal lines both rather vague, more or less interrupted at middle. *Elytra* of about normal outline but much more convex than usual; disc of each elytron slightly impressed about ⅖ from base; basal margin rounded at humeri or at most vaguely subangulate (as usual in genus); lateral margins very narrow; subapical sinuations slight; apices conjointly or slightly independently rounded, not denticulate; inner discal striae very fine, usually almost obsolete anteriorly, but somewhat variable; outer striae and inner ones toward apex moderately impressed; striae vaguely punctulate; intervals flat or slightly convex, 8th and 9th not much modified toward apex. *Lower surface* impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment lobed, outer lobe longer than inner. *Male copulatory organs:* Fig. 29. *Measurements:* length 7.1–7.8; width 2.6–3.2 mm.

Types. Holotype ♂ (Leiden Mus.) and 12 paratypes (some in M.C.Z. No. 28,603) all from Sigi Camp, Snow Mts., **Neth. N. G.**, 1,500 m. (about 4,875 ft.), Feb. 1939 (Toxopeus).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. The very convex form, narrow prothoracic and elytral margins, and fineness of elytral striae on anterior part of disc distinguish this species and give it a remarkable similarity to a very large *Mecyclothorax.* In most other ways the species is very close to the following (*sigi*), from which it may have been derived.

NOTAGONUM SIGI n. sp.

Description. With characters of genus as described above. Form of *Agonum* (*Platynus*); piceous, appendages yellowish, outer margins of prothorax slightly translucent, of elytra scarcely so; surface moderately shining, not or faintly iridescent; microsculpture normal except that of elytra too fine to see at 54×, but elytral surface slightly silky. *Head* .78 & .78 width prothorax; eyes moderately large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* subcordate; width/length 1.39 & 1.41; base/apex 1.21 & 1.27; sides moderately arcuate, moderately sinuate a little before basal angles; latter slightly obtuse, only slightly blunted; lateral margins average; basal foveae average, not sharply defined, slightly roughened; anterior marginal line fine but entire, posterior one light or vague. *Elytra* of normal outline and convexity; lateral margins rather narrow; subapical sinuations rather slight; apices more or less independently rounded to suture, where subangulate but not distinctly denticulate; striae moderately impressed (7th sometimes finer toward base), not or vaguely punctulate; intervals only slightly convex, 8th a little narrowed toward apex, 9th widened and nearly flat toward apex (*i.e.* 8th and 9th intervals not much modified). *Lower surface* with at most a little rather vague punctation; abdomen not pubescent. *Legs:*

4th hind-tarsal segment lobed, outer lobe longer than inner. *Measurements:* length 7.7–7.9; width 2.9–3.0 mm.

Types. Holotype ♂ (Leiden Mus.) and 3 paratypes (1 ♂ in M.C.Z., No. 28,604) all from Sigi Camp, Snow Mts., **Neth. N. G.**, 1,500 m. (about 4,875 ft.), Feb. 27 & 25, 1939, or (1 ♀ only) 1,600 m. (about 5,200 ft.), Dec. 1938 (Toxopeus).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This species is superficially rather like *vaporum* of the same general region, but differs in such important characters as the form of the 9th elytral interval (wide and nearly flat toward apex instead of narrow and very convex) and the non-pubescent abdomen. I have already suggested the possibility that this comparatively normally formed species may be ancestral to the preceding very convex one (*gibbum*).

NOTAGONUM ALTUM n. sp.

Description. With characters of genus as described above, except ♀ with usually only 1 seta each side last ventral segment. Form of *Agonum* (*Platynus*); piceous, appendages brown, lateral margins of prothorax and elytra only slightly paler; microsculpture normal. *Head* .79 & .79 width prothorax (sometimes a little wider); eyes moderately large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* subcordate; width/length 1.48 & 1.44; base/apex 1.16 & 1.21; sides moderately arcuate anteriorly, moderately sinuate about ⅛ of length before base; basal angles more or less obtuse, blunted; lateral margins moderate; basal foveae moderate, roughened or subpunctate; anterior marginal line entire or nearly so but often light at middle, posterior one vague at middle. *Elytra* a little more than usually narrowed toward humeri and a little more convex than usual; lateral margins rather narrow; subapical sinuations slight; apices independently rounded; striae rather deep, not or vaguely punctulate; intervals moderately convex, 8th and 9th not much modified toward apex. *Lower surface* nearly impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment lobed, outer lobe slightly longer than inner. *Secondary sexual characters* normal except ♀ usually with only 1 (not 2) seta each side last ventral segment (at least one ♀ is asymmetrical, with 2 setae on one side, 1 on other). *Measurements:* length 7.7–8.6; width 2.9–3.6 mm.

Types. Holotype ♂ (M.C.Z. No. 28,605) and 25 paratypes all from Chimbu Valley, Bismarck Range, **N-E. N. G.**, some (including type) from the forested zone between 7,000 & 10,000 ft., others from open country between 5,000 & 7,500 ft., but all actually taken under cover beside the Chim River, Oct. 1944 (Darlington).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. The distinguishing characters of this species are sufficiently given in the key.

NOTAGONUM ALTUM IBELE n. subsp.

Description. Similar to typical *altum* (of which see description, above) except in proportions of prothorax, which is relatively slightly narrower in *ibele*, with base especially narrower: in *ibele* the ratio base/apex of prothorax is 1.03 (♂ type), 1.09 (♀), and 1.13 (second ♂); in 6 measured specimens of typical *altum* this ratio is 1.15 to 1.22. Other proportions of *ibele* (♂♂♀) are head/prothorax .80, .79, .84; width/length prothorax 1.40, 1.41, 1.38. The single ♀ of *ibele* has only 1 seta each side last ventral as usual in *altum*. *Measurements:* length 8.8–9.2; width 3.1–3.4 mm. (a little larger but relatively more slender than typical *altum*).

Types. Holotype ♂ (Leiden Mus.) and 2 paratypes (♂, M.C.Z. No. 28,606; ♀, Buitenzorg Mus.) all from Iebele (Ibele) Camp, Snow Mts., **Neth. N. G.**, 2,250 m. (about 7,325 ft.), Nov.–Dec. 1938 (Toxopeus).

Measured specimens. As indicated above.

Notes. Sufficiently compared with typical *altum* above.

NOTAGONUM MARGARITUM n. sp.

Description. With characters of genus as described above. Form between *Agonum* s. s. and *Platynus*; piceous-black with pearly lustre, appendages brownish-yellow, lateral margins of prothorax and elytra moderately pale-translucent (elytra the less so); surface moderately shining, moderately (not strongly) iridescent especially on elytra; microsculpture apparently normal but almost too fine to see at 54×. *Head* .74 & .74 width prothorax; eyes large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* somewhat transverse; width/length 1.42 & 1.40; base/apex 1.26 & 1.29; sides arcuate for most of length, slightly or not distinctly sinuate before base; posterior angles obtuse, blunted or narrowly rounded; lateral margins moderate; basal foveae rather deep, scarcely roughened, not punctate; anterior marginal line fine but entire and distinct at middle, posterior one less distinct. *Elytra* of about normal outline and convexity; lateral margins moderate; subapical sinuations slight or moderate; apices independently rounded (sometimes subangulate opposite 3rd intervals), each with a strong denticle at suture; striae moderately impressed, usually more or less distinctly punctulate;

ntervals a little convex, 8th and 9th not much modified toward apex. *Lower surface* impunctate or slightly or vaguely punctate at sides of sterna; abdomen not pubescent. *Legs:* 4th hind-tarsal segment briefly lobed, outer lobe slightly longer than inner. *Measurements:* length 7.0–9.0; width 2.7–3.3 mm.

Types. Holotype ♂ (M.C.Z. No. 28,607) and 10 paratypes from Nadzab, **N-E. N. G.**, July 1944 (Darlington). Also the following additional paratypes: **Papua:** 1, Mafulu, 4,000 ft., Dec. 1933 (Cheesman). **N-E. N. G.:** 1, Finschhafen, Apr. 20, 1944 (E. S. Ross, California Acad.); 13, Chimbu Valley, Bismarck Range, 5,000–7,500 ft., Oct. 1944 (Darlington). **Neth. N. G.:** 3, vicinity of Hollandia, July–Sept. 1944 (Darlington); 1, Sabron, Cyclops Mts., 930 ft., May–June 1936 (Cheesman); 12, Cyclops Mts. (including Mt. Cyclops and Mt. Lina), 3,400(or 3,500)–4,500 ft., Mar. 1939 (Cheesman); 1, Rattan Camp, Snow Mts., 1,150 m. (about 3,750 ft.), Feb.–Mar. 1939 (Toxopeus); 2, Baliem Camp, Snow Mts., 1,600 & 1,700 m. (about 5,200 & 5,525 ft.), Dec. & Nov. 16–27, 1938 (Toxopeus).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Nadzab.

Notes. The comparatively weak subapical sinuations of the elytra, usually distinctly iridescent surface, and frequently (but not always) punctulate elytral striae distinguish this species from other similar ones. In doubtful cases and in the absence of comparative material the following details should aid in distinguishing this from other species with denticulate but otherwise unarmed elytral apices: 4th hind-tarsal segment lobed (not simply emarginate as in *subpunctum*); anterior transverse marginal line of pronotum entire and distinct at middle (not vague or interrupted at middle as in *dentellum*); and elytra not transversely impressed before middle (as in *subimpressum*).

NOTAGONUM SUBPUNCTUM n. sp.

Description. With characters of genus as described above. Form of *Agonum s. s.*; black or piceous, appendages dark-brown, outer margins of prothorax and elytra slightly translucent; surface moderately shining, not distinctly iridescent; microsculpture of pronotal foveae less distinct than usual, of elytra more distinct, coarse, and less transverse than usual. *Head* .69 & .67 width prothorax; eyes large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* rather large; width/length 1.45 & 1.47; base/apex 1.24 & 1.29; sides arcuate anteriorly, nearly straight and converging posteriorly, slightly or not sinuate before base; posterior angles obtuse, blunted; lateral margins a little wider than usual and more elevated near base; basal foveae rather deep, usually irregularly punctate, with some punctures usually also before foveae near pronotal margins; anterior marginal line entire, basal one vague. *Elytra* of about normal outline and convexity; outer margins moderately wide; subapical sinuations strong; apices independently rounded, bluntly denticulate at suture; striae deep, impunctate; intervals somewhat convex, 8th narrowed and very convex toward apex, 9th only slightly widened and moderately convex toward apex. *Lower surface* impunctate or nearly so; abdomen not pubescent. *Legs:* 4th hind-tarsal segment simple emarginate, not lobed. *Measurements:* length 6.5–7.4; width 2.4–2.7 mm.

Types. Holotype ♂ (M.C.Z. No. 28,608) and 16 paratypes all from Dobodura, **Papua**, Mar.–July 1944 (Darlington).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This species is instantly distinguishable from superficially rather similar ones (*margaritum, dentellum, subimpressum*) by the simply emarginate rather than lobed 4th hind-tarsal segment. The unusually heavy micro-reticulation of the elytral surface should aid in recognition of the typical form of this species, but not of the following subspecies.

NOTAGONUM SUBPUNCTUM CAPITIS n. subsp.

Description. Nearly the same as typical *subpunctum* (of which see description, above) in form, proportions, and most detailed characters, including simply emarginate 4th hind-tarsal segment (Fig. 19), but larger, with elytra much more finely micro-reticulate, the meshes barely visible at 54×. Proportions of measured specimens: head/prothorax .69 & .69; width/length prothorax 1.46 & 1.43; base/apex prothorax 1.20 & 1.24. *Measurements:* length 7.7–8.5; width 2.8–3.2 mm.

Types. Holotype ♂ (M.C.Z. No. 28,609) and 10 paratypes all from Sansapor (Vogelkop), **Neth. N. G.**, Aug. 1944 (Darlington), taken in wet places in forested country.

Other material. **Neth. N. G.:** 1, Maffin Bay, Aug. 1944 (Darlington) 1, Hollandia, June 10, 1945 (from K. M. Fender, M.C.Z.).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. Sufficiently compared with typical *subpunctum* above and in the key to species of *Notagonum.*

NOTAGONUM DENTELLUM n. sp.

Description. With characters of genus as described above. Form of rather broad *Agonum s. s.*; piceous-black, appendages yellow or brownish-yellow, lateral margins of prothorax and elytra yellow;

surface moderately shining, slightly iridescent; microsculpture normal. *Head* .74 & .73 width prothorax; eyes large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* moderately transverse; width/length 1.43 & 1.47; base/apex 1.26 & 1.21; sides arcuate for much of length, then moderately (somewhat variably) sinuate near base; posterior angles obtuse, blunted; lateral margins rather wide; basal foveae moderately deep, slightly roughened; anterior and posterior marginal lines irregular, faint, usually incomplete. *Elytra* of about normal outline and convexity, not or very little impressed on disc; lateral margins slightly wider than usual; subapical sinuations rather strong; apices typically narrowly subtruncate (but exact form somewhat variable), usually denticulate at suture; striae moderately deep, not or slightly punctulate; intervals slightly convex, 8th and 9th not much modified toward apex. *Lower surface* impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment lobed, outer lobe longer than inner. *Male copulatory organs:* Fig. 30. *Measurements* (Dobodura series): length 7.3–8.5; width 2.8–3.4 mm. (some smaller specimens from other localities).

Types. Holotype ♂ (M.C.Z. No. 28,610) and 11 paratypes from Dobodura, **Papua**, Mar.–July 1944 (Darlington). Additional paratypes as follows: **N-E. N. G.:** 1, Lae, Oct. 1944 (Darlington); 5, Nadzab, July 1944 (Darlington); 12, Aitape, Aug. 1944 (Darlington). **Neth. N. G.:** 10, vicinity of Hollandia, July–Sept. 1944 (Darlington); 3, Maffin Bay, Aug. 1944 (Darlington).

Other material. **Papua:** 4, Dobodura, Mar.–July 1944 (Darlington) (more slender than typical specimens, with elytra somewhat impressed at or slightly before middle). **N-E. N. G.:** 2, Nadzab, July 1944 (Darlington) (slender, elytra slightly impressed and not denticulate); 1, Surprise Creek, Morobe Dist., Oct. 4 (Stevens, M.C.Z.) (broad, sides of prothorax strongly sinuate). **Neth. N. G.:** 1, vicinity of Hollandia, July–Sept. 1944 (Darlington) (more slender and with elytral striae more strongly punctulate than usual); 1, Mt. Cyclops, 3,500 ft., Mar. 1936 (Cheesman) (large, with margins and appendages darker than usual); 1, Araucaria Camp, Snow Mts., 800 m. (about 2,600 ft.), Mar. 1939 (Toxopeus) (rather small and with sides of prothorax more sinuate than usual); and 1, Camp 1, Mt. Nok, Waigeo Is., 2,500 ft., May 1938 (Cheesman) (rather small, with head relatively large and prothorax smaller and with sides more sinuate than usual, and with elytral apices squarely truncate). More material is needed to clarify the status of these forms. A form of this species occurs also at Cape Gloucester, **New Britain** (Darlington); and the following subspecies is, so far as known, localized on the Bismarck Range, N-E. N. G.

Measured specimens. The ♂ holotype and 1 ♀ paratype from Dobodura.

Notes. Typical specimens of this species are identifiable by characters given in the key to species of *Notagonum.* The species is, however, a variable one, as the notes given under "Other material" suggest. This is one of the species in which the elytral denticles are variable, being acute, blunt, or faint in different individuals even in the type series, and completely absent in a few aberrant individuals.

NOTAGONUM DENTELLUM CHIMBU n. subsp.

Description. Generally similar to typical *dentellum* (of which see description, above) but larger; eyes slightly less prominent; prothorax relatively smaller, with sides usually more sinuate and basal angles usually more distinct. These differences are such that, although they give the insect a somewhat different appearance, they change its proportions very little. The proportions of the measured specimens are head/prothorax .74 & .73; width/length prothorax 1.43 & 1.45; base/apex prothorax 1.23 & 1.15. The elytra of *chimbu* have slightly stronger subapical sinuations than in typical *dentellum* and are a little more coarsely striate, and the intervals are flatter toward apex. *Measurements:* length 8.4–9.7; width 3.2–3.8 mm.

Types. Holotype ♂ (M.C.Z. No. 28,611) and 17 paratypes all from Chimbu Valley, Bismarck Range, **N-E. N. G.**, 5,000–7,500 ft., Oct. 1944 (Darlington).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. Sufficiently compared with typical *dentellum* above.

NOTAGONUM SUBIMPRESSUM n. sp.

Description. With characters of genus as described above. Form of *Agonum s. s.*; piceous-black, appendages brownish-piceous, outer antennal segments paler brown, lateral margins of prothorax only slightly translucent, of elytra even less so; surface moderately shining, not or slightly iridescent; microsculpture normal, but light and restricted on head and prothorax. *Head* .74 & .73 width prothorax; eyes large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* of average size; width/length 1.44 & 1.50; base/apex 1.39 & 1.36; sides arcuate for much of length, nearly straight and converging and usually slightly sinuate toward base; basal angles obtuse, blunted or narrowly rounded; lateral margins average; basal foveae rather deep, slightly roughened, sometimes vaguely punctate; anterior marginal line entire or nearly so, posterior one entire or vague at middle. *Elytra* of average outline and convexity, but rather strongly impressed across disc about ⅓ from base; lateral margins normal; subapical sinuations rather strong; apices independently rounded or sometimes vaguely angulate about opposite 3rd interval, rather inconspicuously denticulate at suture; striae moderately impressed, not or vaguely punctulate; intervals slightly convex, 8th and 9th not much modified toward apex. *Lower surface* nearly impunctate; abdomen with a very little fine pubescence near middle of some segments. *Legs:* 4th hind-tarsal segment lobed, outer lobe longer than inner. *Measurements:* length 8.1–8.7; width 3.1–3.5 mm.

Types. Holotype ♂ (M.C.Z. No. 28,612) and 22 paratypes from Dobodura, **Papua**, Mar.–July 1944 (Darlington), taken in a variety of damp places. Additional paratypes as follows: **Papua:** 1, Oro Bay, Dec. 1943 (Darlington); 1, Kokoda, 1,200 ft., Sept. 1933 (Cheesman); 10, Milne Bay, Dec. 1943 (Darlington). **Neth. N. G.:** 18, Hollandia, July–Sept. 1944 (Darlington), and 1, same locality, Apr. 1945 (Malkin, U.S.N.M.); 1, Araucaria Camp, Snow Mts., 800 m. (about 2,600 ft.), Mar. 1939 (Toxopeus); 7, Wasian, Sept. 1939 (Wind, M.C.Z.).

Other material. Six, Cape Gloucester, **New Britain**, Jan.–Feb. 1943 (Darlington).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Dobodura.

Notes. Several other species of *Notagonum* have the elytral disc more or less impressed before the middle, but no other so much as this, which has almost a sway-backed appearance. This character, together with the rather dark legs and antennal bases, makes this species easy to recognize even superficially. Other distinguishing characters of the species are given in the key to species of *Notagonum.*

NOTAGONUM PALUDUM n. sp.

Description. With characters of genus as described above. Form of broad *Agonum s. s.*, but small; piceous-black, appendages brownish-piceous, lateral margins of prothorax and elytra brownish-translucent; surface moderately shining, not distinctly iridescent; microsculpture nearly normal but that of pronotum very light, that of elytra more distinct. *Head* .67 & .65 width prothorax; eyes moderately large and prominent, with posterior supraocular setae a trifle behind line of their posterior edges. *Prothorax* relatively large; width/length 1.45 & 1.45; base/apex 1.29 & 1.28; sides arcuate for much of length, straight and converging and sometimes slightly sinuate before base; posterior angles obtuse, slightly blunted; lateral margins rather wide; basal foveae moderately deep, scarcely roughened; anterior marginal line entire, posterior one lighter or vague. *Elytra* of about normal outline and convexity, each somewhat impressed before middle; lateral margins rather wide (in genus); subapical sinuations rather strong; apices each bi-angulate or bi-denticulate (the angles or denticles about opposite 3rd and sutural intervals), with apex between angles or denticles emarginate; striae moderately impressed, not or faintly punctulate; intervals only slightly convex, more so laterally and apically (as usual), 8th and 9th not much modified toward apex. *Lower surface* impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment scarcely more than emarginate, but with very small inconspicuous lobes, the outer longer than inner. *Measurements:* length 5.6–6.5; width 2.2–2.5 mm.

Types. Holotype ♂ (M.C.Z. No. 28,613) and 27 paratypes all from Dobodura, **Papua**, Mar.–July 1944 (Darlington), taken among wet dead leaves by pools in forest.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This distinct little species should be easily recognized by characters given in the key to species of *Notagonum*.

NOTAGONUM PALUDUM VELUM n. subsp.

Description. Generally similar to typical *paludum* (of which see description, above); differing only slightly in size (averaging slightly larger), proportions, and most other details (elytral striae slightly deeper, etc.); but easily distinguished by elytral microsculpture. In typical *paludum* the micro-reticulations on the elytra are coarser than usual and are easily seen in all specimens at 54×, but in the present new subspecies the elytral reticulations are so fine as to be barely or not visible at the same magnification. Proportions of measured specimens: head/prothorax .64 & .64; width/length prothorax 1.54 & 1.61; base/apex prothorax 1.24 & 1.26. *Measurements:* length 6.3–6.6; width about 2.5 mm.

Types. Holotype ♂ (M.C.Z. No. 28,614) and 4 paratypes (all ♀♀) all from Aitape, **N-E. N. G.**, Aug. 1944 (Darlington), taken in a flood in forested or formerly forested country.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. Sufficiently compared with typical *paludum* above.

NOTAGONUM MALKINI n. sp.

Description. With characters of genus as described above. Form of rather broad *Agonum s. s.*; piceous-black, legs and antennal bases brownish-piceous, outer segments of antennae brown, lateral margins of prothorax slightly paler or translucent, lateral margins of elytra scarcely paler; surface moderately shining, moderately iridescent; microsculpture normal, light. *Head* .68 & .68 width prothorax; eyes large and very prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* rather large and rather transverse; width/length 1.54 & 1.55; base/apex 1.35 & 1.38; sides arcuate for much of length, then straight and converging or very slightly sinuate to posterior angles; latter obtuse, slightly blunted; lateral margins wide but not sharply set off from disc; basal foveae rather wide, moderately deep, only slightly roughened; anterior marginal line entire or slightly interrupted at middle, posterior one vague. *Elytra* rather broad, of about normal outline and convexity, not distinctly impressed on disc; lateral margins slightly wider than usual; subapical sinuations rather strong; apices each minutely angulate about opposite 3rd interval (which turns somewhat toward suture), then emarginate to denticulate sutural angles; outer angle or denticle slightly more prominent than sutural denticle; striae moderately impressed, not distinctly punctulate; intervals slightly convex, 8th narrowed and much more convex toward apex, 9th somewhat widened and somewhat flattened toward apex (but these intervals still not very much more modified than usual). *Lower surface* nearly impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment emarginate, scarcely lobed. *Male copulatory organs:* Fig. 31. *Measurements:* length 7.6–8.2; width 3.0 or slightly more mm.

Types. Holotype ♂ (M.C.Z. No. 28,615) from vicinity of Hollandia, **Neth. N. G.**, July–Sept. 1944 (Darlington), and 1 ♀ paratype from the same locality, Apr. 1945 (Borys Malkin, U.S.N.M.).

Measured specimens. The types.

Notes. Sufficiently distinguished from other bi-denticulate species in the key to species of *Notagonum.* I have considered whether the two specimens described above can be bi-denticulate individuals of a normally uni-denticulate species, but they seem not to be. They differ from *subpunctum* not only in form of elytral apices but also in lack of distinct punctation in the pronotal foveae and in other ways; and they differ from *dentellum* not only in form of elytral apices but also in lack of conspicuous pale lateral elytral margins, in lack of distinct lobes on the 4th hind-tarsal segment, and in other ways. They are distinguished from bi-denticulate individuals of *margaritum* in the key.

NOTAGONUM IRIDIOR n. sp.

Description. With characters of genus as described above. Form of *Agonum s. s.*; piceous-black, legs and antennal bases slightly more reddish-piceous, outer antennal segments browner, lateral margins of prothorax and elytra somewhat translucent; surface moderately shining, elytra more iridescent than in any other species of genus except perhaps *angulum* (below); microsculpture normal but finer than usual. *Head* .71 & .74 width prothorax; eyes large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* rather transverse-subcordate, with apex more deeply emarginate than usual; width/length 1.48 & 1.44; base/apex 1.28 & 1.18; sides rounded for most of length, sinuate near posterior angles; latter obtuse (partly because of rounding of sides of base), blunted; lateral margins rather wide, flatter than usual anteriorly; basal foveae rather deep, only slightly roughened, vaguely punctate; anterior marginal line entire or nearly so, posterior one vague. *Elytra* of about normal outline and convexity, not or faintly impressed on disc; lateral margins moderate; subapical sinuations rather weak; apices each angulate opposite 3rd interval, then emarginate to sutural angle; latter denticulate; striae less impressed than usual, not distinctly punctulate; intervals nearly flat, 8th and 9th not much modified toward apex. *Lower surface* slightly punctate at sides of sterna; abdomen not pubescent. *Legs:* 4th hind-tarsal segment emarginate, not lobed. *Measurements:* length 8.0–9.0; width 3.0–3.5 mm.

Types. Holotype ♀ (M.C.Z. No. 28,616) and 3 paratypes (all ♀♀) all from Wasian, **Neth. N. G.**, Sept. 1939 (R. G. Wind).

Measured specimens. The ♀ holotype and 1 ♀ paratype.

Notes. The characters for recognition of this species are the iridescence of the elytra and the rather deep emargination of the front of the prothorax. Of the less obvious characters, the form of the 4th hind-tarsal segment (simply emarginate) is noteworthy, though repeated in a few other species of the genus.

NOTAGONUM ADDENDUM n. sp.

Description. With characters of genus as described above. Form of rather broad *Agonum s. s.*; brownish-black, appendages brown, lateral margins of prothorax and elytra moderately translucent; surface moderately shining, not iridescent; microsculpture normal. *Head* .66 & .69 width prothorax; eyes large and prominent, with posterior supraocular setae a little before line of their posterior edges. *Prothorax* rather large and wide; width/length 1.52 & 1.53; base/apex 1.28 & 1.32; sides rather strongly arcuate for much of length, nearly straight and strongly converging and sometimes slightly sinuate before very obtuse but distinguishable basal angles; lateral margins rather wide especially toward base, moderately reflexed; basal foveae average, roughened but not distinctly punctate; anterior marginal line entire, posterior one more or less entire but vague at middle. *Elytra* rather broad, of normal outline and convexity, not distinctly impressed on disc; lateral margins rather wide (in genus); subapical sinuations moderate; apices each strongly angulate about opposite 3rd interval (this angle more prominent than the sutural one), then obliquely subtruncate or slightly emarginate to slightly denticulate sutural angle; striae moderately impressed, not distinctly punctulate; intervals nearly flat or slightly convex, 8th and 9th not much modified toward apex. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment deeply emarginate, with small outer but scarcely any inner lobe. *Measurements:* length 6.8–7.6; width 2.8–3.0 mm.

Types. Holotype ♂ (M.C.Z. No. 28,617) and 3 ♂♂ paratypes from Dobodura, **Papua**, Mar.–July 1944 (Darlington); and 2 paratypes from Mt. Nok, Waigeo Is., **Neth. N. G.**, 2,500 ft., Apr. & May 1938 (Cheesman).

Measured specimens. The ♂ holotype and 1 ♂ paratype from Dobodura.

Notes. This species is sufficiently distinguished from others in the key to species of *Notagonum*, above. In form and in shape of elytral apices it is so much like *Altagonum vallicola* n. sp. (below) that I at first thought it might be a form of that species which had retained the anterior pronotal and anterior dorsal elytral setigerous punctures, but the present new species differs from *vallicola* not only in possessing these setae and punctures but also in being less black in color, with more translucent lateral prothoracic and elytral margins, and in having small but distinct outer lobes on the 4th hind-tarsal segments.

NOTAGONUM ANGULUM n. sp.

Description. With characters of genus as described above. Form of rather slender *Agonum* or *Platynus*; piceous-black, browner-piceous below, appendages yellow or brownish-yellow, lateral margins of prothorax rather strongly pale-translucent, of elytra scarcely so; surface moderately shining and (especially elytra) moderately iridescent; microsculpture probably nearly normal but very light and restricted on pronotum and too fine to distinguish in detail at 54× on elytra. *Head* .77 & .80 width prothorax; eyes moderately large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax:* width/length 1.30 & 1.30; base/apex 1.18 & 1.23; sides arcuate anteriorly, nearly straight and converging posteriorly, usually slightly sinuate near posterior angles; latter obtuse, blunted or narrowly rounded; lateral margins moderate; basal foveae moderate, only slightly roughened; anterior marginal line entire, posterior one interrupted or vague at middle. *Elytra* rather long but otherwise of normal outline and convexity, not or slightly impressed on disc; lateral margins normal; subapical sinuations moderate; apices each strongly, about rectangularly angulate (and sometimes subdenticulate) opposite 2nd or 3rd interval, then emarginate to more or less denticulate sutural angle; striae moderately deep, not distinctly punctulate; intervals slightly or moderately convex, 8th and 9th not much modified toward apex. *Lower surface* impunctate or nearly so; abdomen not pubescent. *Legs:* 4th hind-tarsal segment lobed, outer lobe longer than inner. *Measurements:* length 8.2–9.7; width 2.9–3.4 mm.

Types. Holotype ♂ (Leiden Mus.) and 16 paratypes from Rattan Camp, Snow Mts., **Neth. N. G.**, 1,150 & 1,200 m. (about 3,750 & 3,900 ft.), Feb.–Mar. 1939 (Toxopeus); and 6 paratypes from Sigi Camp, Snow Mts., 1,500 m. (about 4,875 ft.), Feb. 1939 (Toxopeus). (Some paratypes in M.C.Z., No. 28,618).

Other material. One teneral, Sigi Camp (as above); 1, Chimbu Valley, Bismarck Range, **N-E. N. G.**, 5,000–7,500 ft., Oct. 1944 (Darlington); 1, Mafulu, **Papua**, 4,000 ft., Dec. 1933 (Cheesman).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Rattan Camp.

Notes. This fine species is easily known by its rather slender form (compared with related species), pale-translucent prothoracic margins, iridescent elytra, and strongly angulate elytral apices.

NOTAGONUM SUBANGULUM n. sp.

Description. With characters of genus as described above. Form of rather slender *Agonum s. s.*; brownish-piceous (perhaps sometimes darker), appendages brownish-yellow, lateral margins of prothorax rather strongly translucent, of elytra much less so; surface moderately shining, only faintly iridescent; microsculpture normal, a little more distinct than in *angulum*. *Head* .77 & .77 width prothorax; eyes large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* somewhat transverse; width/length 1.42 & 1.41; base/apex 1.36 & 1.33; sides arcuate anteriorly, converging and straight or faintly sinuate posteriorly; posterior angles obtuse, blunted or narrowly rounded; lateral margins moderate; basal foveae moderate, scarcely roughened; anterior marginal line entire, posterior one almost so. *Elytra* a little longer than usual but otherwise normal in outline and convexity; lateral margins average; subapical sinuations moderate; apices each strongly but a little obtusely angulate about opposite 3rd interval, then oblique forward to minutely or vaguely denticulate sutural angle; striae moderately impressed, not distinctly punctulate; intervals nearly flat or slightly convex, 8th and 9th not much modified toward apex. *Lower surface* not distinctly punctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment lobed, outer lobe longer than inner. *Measurements:* length 7.7–8.2; width 2.7–3.0 mm.

Types. Holotype ♂ (Leiden Mus.) and 1 ♂ paratype (M.C.Z. No. 28,619) both from Sigi Camp, Snow Mts., **Neth. N. G.**, the type at 1,600 m. (about 5,200 ft.), Feb. 20, 1939, and the paratype at 1,500 m. (about 4,875 ft.), Feb. 1939 (both, Toxopeus).

Measured specimens. The types.

Notes. This species resembles the preceding (*angulum*) in a general way but differs in several details, especially in having a wider prothorax with relatively wider base (*cf.* ratios given in descriptions) and in having much less iridescent elytra.

NOTAGONUM SUBRUFUM n. sp.

Description. With characters of genus as described above, except hind-tarsal sole with a nearly regular row of bristles each side, with middle of sole broadly bare. Form of slender *Agonum* (*Platynus*); rather dark rufous (elytra a little darker than head and prothorax), appendages yellow, lateral margins of prothorax and elytra moderately translucent; surface moderately shining, not iridescent; microsculpture faint on head, otherwise normal. *Head* .82 & .79 width prothorax; eyes moderately large and prominent, with posterior supraocular setae just behind line of their posterior edges. *Prothorax* rather narrow, subcordate; width/length 1.20 & 1.23; base/apex 1.12 & 1.11; sides rather weakly arcuate for much of length, then straight and converging posteriorly, and slightly or moderately sinuate before base; posterior angles obtuse (partly because sides of base obliquely rounded), slightly blunted; lateral margins average; basal foveae rather deep, slightly roughened, and basal area between foveae slightly depressed and roughened; anterior marginal line entire or slightly interrupted at middle, posterior one rather vague. *Elytra* rather narrow but otherwise of about normal outline and convexity; lateral margins rather narrow; subapical sinuations absent (except as margins turn onto spines); apices each with a spine opposite 3rd interval (the spine about as long as width of 1½ discal elytral intervals), with sutural angles broadly rounded, not denticulate; striae rather deep, not distinctly punctulate; intervals moderately convex, 8th and 9th not much modified toward apex. *Lower surface* impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment emarginate, very briefly (scarcely) lobed, outer lobe very slightly longer than inner; sole of hind tarsus as described above. *Male copulatory organs:* Fig. 32. *Measurements:* length 7.2–7.4; width 2.3 mm.

Types. Holotype ♂ (Leiden Mus.) and 1 ♀ paratype (M.C.Z. No.

28,620) both from Rattan Camp, Snow Mts., **Neth. N. G.**, 1,200 m. (about 3,900 ft.), Feb.–Mar. 1939 (Toxopeus).

Measured specimens. The types.

Notes. This fine little species is not closely related to any other known to me. It is sufficiently characterized in the key to species of *Notagonum*. It is probably not related to *Lorostemma*, although the hind tarsi are similarly clothed below.

NOTAGONUM SPINULUM n. sp.

Description. With characters of genus as described above. Form of broad *Agonum s. s.*; black, appendages blackish, outer segments of antennae brown, lateral margins of prothorax and elytra not paler; surface moderately shining, not distinctly iridescent; microsculpture normal, light. *Head* .64 & .63 width prothorax; eyes large and prominent, with posterior supraocular setae between their posterior edges. *Prothorax* large and wide; width/length 1.52 & 1.59; base/apex 1.40 & 1.39; sides arcuate for most of length, usually slightly sinuate before base; posterior angles obtuse, more or less rounded; lateral margins relatively wide but less reflexed or elevated than usual; basal foveae wide, only moderately deep, only slightly roughened; anterior marginal line entire or nearly so, posterior one vague or interrupted at middle. *Elytra* broader than usual but otherwise of normal outline and convexity; lateral margins rather wide (in genus); subapical sinuations rather strong; apices each with a spine about opposite 3rd interval (spines about as long as width of 1½ discal elytral intervals), then emarginate to denticulate sutural angle; striae rather lightly impressed, not distinctly punctulate; intervals flat on disc, slightly convex laterally and apically, 8th and 9th not much modified toward apex. *Lower surface* impunctate or nearly so; abdomen not pubescent. *Legs:* 4th hind-tarsal segment emarginate and with very short lobes below, outer lobe a little longer than inner. *Male copulatory organs:* Fig. 33. *Measurements:* length 7.3–8.4; width 2.8–3.3 mm.

Types. Holotype ♂ (M.C.Z. No. 28,621) and 25 paratypes all from Dobodura, **Papua**, Mar.–July 1944 (Darlington), taken among dead leaves and in leaf mold on the ground in heavy rainforest.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. The relatively broad form, black color, and spined elytra distinguish this species from all other *Notagonum* except the following one (*subspinulum*), *q.v.*

NOTAGONUM SUBSPINULUM n. sp.

Description. With characters of genus as described above. Form of rather broad *Agonum s. s.*; black, appendages brownish, lateral margins of prothorax only slightly translucent, of elytra not distinctly so; surface moderately shining, not distinctly iridescent; microsculpture normal. *Head* .67 & .68 width prothorax; eyes large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* moderately large; width/length 1.43 & 1.48; base/apex 1.33 & 1.35; sides arcuate anteriorly, nearly straight and converging posteriorly, slightly sinuate before base; posterior angles obtuse and finely blunted but somewhat better defined than in *spinulum*; lateral margins moderately wide, more reflexed than in *spinulum*; basal foveae rather deep, not much roughened; anterior marginal line entire, posterior one vague or interrupted at middle. *Elytra* of about normal outline and convexity, usually with disc a little impressed about ⅓ from base; lateral margins average; subapical sinuations rather strong; apices each with a very short spine or long tooth about opposite 3rd interval (spines about as long as width of 1 discal elytral interval), then emarginate to finely denticulate sutural angle; striae rather deep, not punctate; intervals moderately convex, 8th and 9th not much modified toward apex. *Lower surface* impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment emarginate, not lobed beneath. *Measurements:* length 6.8; width 2.5 mm.

Types. Holotype ♂ (M.C.Z. No. 28,622) and 1 ♂ paratype both from Dobodura, **Papua**, Mar.–July 1944 (Darlington).

Measured specimens. The types.

Notes. This species is generally similar to and probably related to the preceding (*spinulum*). It is from the same locality; I do not know whether it is from the same ecological habitat. It differs from *spinulum* in being smaller, less wide, with prothorax proportionately narrower (*cf.* proportions given in descriptions) and with less wide and more reflexed lateral margins and somewhat better defined posterior angles, elytra much more deeply striate and with shorter apical spines, and 4th hind-tarsal segment without the short lobes which are present in *spinulum.*

Genus COLPODES Macl.

Macleay 1825, Annulosa Javanica, p. 17.

Csiki 1936, Coleop. Cat., Carabidae, Harpalinae **5**, p. 745 (see for synonyms and additional references).

Jeannel 1948, Coléoptères Carabiques de la Région Malgache, Part 2, pp. 514, 515, 516.

Diagnosis. See key to genera.

Description. None required here. Genus as here restricted has *inner wings* always fully developed; seta-formula ++, ++, (+) (+)+; *secondary sexual characters* normal except in *rex* (which see); *male copulatory organs* of several species figured (Figs. 34–40).

Genotype. *C. brunneus* Macl. (*op. cit.*, p. 17, Pl. 1, Fig. 3) of Java. It should be noted that the species figured as *brunneus* by Jeannel (*op. cit.*, p. 514, Fig. 235a) is not that species and is not even closely related to it. True *brunneus* is apparently still known only from the single type, and is a peculiar, large, brown form, with small but abruptly prominent eyes and denticulate sutural angles of elytra. I have myself examined the type briefly at the British Museum, and I am indebted to Mr. E. B. Britton for additional notes on it.

Generic distribution. As here limited the genus is widely distributed from the Orient to northern Australia. Very many species of other tropical areas are now assigned to the genus, but it remains to be seen whether or not they are really congeneric with the Oriental forms.

Notes. It is obvious that the mass of diverse species now included in *Colpodes* should be broken up into genera or subgenera, and I have taken some steps toward breaking it up here, but only so far as the New Guinean forms are concerned. The eleven New Guinean species that I am leaving in *Colpodes* still present such a diversity of characters that I feel sure a further division will be necessary. It may well prove that none of the eleven is really congeneric with the genotype.

Jeannel (*loc. cit.*) has offered a table of the principal Oriental genera of Anchomenini (Agonini) which is concerned largely with components of the old *Colpodes*. I have already discussed this table, above, in notes under the tribe Agonini. It is superficial and otherwise unsatisfactory. In my opinion *Colpodes* will not be finally, satisfactorily divided until a large number of forms from many different regions are carefully studied and compared. This is something I should like to do some day, but it is far too big a task to undertake here.

Colpodes violaceus is a common lowland species. The other New Guinean species here assigned to the genus seem particularly characteristic of the lower and middle mountain slopes. In habits, they, or at least the ones that I know in life, are more arboreal or subarboreal than the species of *Notagonum*.

Key to the Species of Colpodes of New Guinea

1. Head relatively short, with short mandibles; prothorax wide, ½ or more wider than long, with base ⅓ or more wider than apex; size small, about 10 mm. or less; (form broad; color purple; each elytron with an apical spine about opposite 2nd interval) (p. 160) . . . . *violaceus*

— Head longer, with relatively longer mandibles; prothorax narrower, with relatively narrower base; size larger, except in small specimens of *laetus* 2

2. Each elytron spined at outer angle (outside the subapical sinuation) as well as at sutural angle; (length about 13½ to 15 mm.; color blue or purple) (p. 161) .... *saphyrinus sloanei*

— Outer angles of elytra not spined, rarely angulate, usually not defined . . 3

3. Each elytron with a spine at sutural angle, the spine longer than width of a discal elytral interval; (length 11.6–13.8 mm.; form slender, depressed; color rufopiceous; elytra very deeply striate) (p. 162) .... *helluo*

— Elytra either not spined or with spines not at sutural angles (but latter sometimes denticulate) 4

4. Color at least partly green, blue, or purplish 5

— Color black or piceous 8

5. Strikingly bicolored: red, elytra blue or greenish with red apices; length about 9½–13 mm. (p. 163) .... *laetus*

— Not thus bicolored; usually larger 6

6. Elytra not spined (but denticulate at sutural angles) and with outer intervals not compressed toward apex; length 13–17 mm. (p. 164) . . . . *habilis*

— Elytra *either* with outer intervals compressed toward apex *or* with short apical spines about opposite 3rd intervals; size still larger 7

7. Elytra with outer intervals (especially 8th) compressed to narrow carinae toward apex; apices not spined (but denticulate at sutural angles); length 18–21 mm. (p. 165) .... *bennigseni*

— Elytra with outer intervals not compressed toward apex; each elytron with a short apical spine about opposite 3rd interval; length 19–23 mm. (p. 167) .... *rex*

8. Elytra with outer angles (outside subapical sinuations) well defined, finely sub-rectangular (elytral apices also spined about opposite 3rd intervals) (p. 169) .... *antedens*

— Elytra with outer angles not defined 9

9. Elytra with basal margin incomplete, only 1 dorsal puncture (the posterior one) present on 3rd interval, and with apices conspicuously angulate about opposite 2nd intervals, with points of angles usually slightly produced (p. 170) .... *acuticauda*

— Elytra with anterior margin entire, 3 dorsal punctures on 3rd interval, and apices not conspicuously angulate 10

10. Elytra with strong subapical sinuations, and denticulate at sutural angles; length 13.6–14.8 mm. (p. 171) .... *sinuicauda*

— Elytra with weak subapical sinuations, and not distinctly denticulate at sutural angles; length about 17–21 mm. (p. 172) .... *simplicicauda*

COLPODES VIOLACEUS Chd.

Chaudoir 1859, Ann. Soc. Ent. France (3) **7**, p. 351.

Andrewes 1930, Cat. Indian Carabidae, p. 126 (see for additional references).

Description. None required here. See key, above, for recognition-characters. *Male copulatory organs:* Fig. 34.

Type. From the **Aru** ("Arrou") **Islands**; Andrewes (*loc. cit.*) indicates that he has seen it in the Oberthür Collection.

Occurrence in New Guinea. **Papua:** 10, Milne Bay, Dec. 1943 (Darlington); 1, Oro Bay, Dec. 1943-Jan. 1944 (Darlington); 11, Dobodura, Mar.-July 1944 (Darlington); 9, Kokoda, 1,200 & 1,300 ft., May, Aug., Sept., & Oct. 1933 (Cheesman). **N-E. N. G.:** 1, Aitape, Aug. 1944 (Darlington). **Neth. N. G.:** 4, vicinity of Hollandia, July-Sept. 1944 (Darlington), and 2, same locality, Apr. 1945 (Malkin, U.S.N.M.); 1, Mt. Nomo, 700 ft., Feb. 1936 (Cheesman); 2, Bewani Mts. (1 at 400 m., or about 1,300 ft.), July & Sept. 1937 (W. Stüber, British Mus.); 1, Sabron, Cyclops Mts., 1,200 ft., May 15, 1936 (Cheesman); 1, Geelvink Bay (Raffray & Maindron, Paris Mus.); 2, Bernhard Camp, Snow Mts., 50 m. (about 160 ft.), July-Nov. 1938 (J. Olthof, Neth. Ind.-American Exp.); 14, Araucaria Camp, Snow Mts., 800 m. (about 2,600 ft.), Mar. 1939 (Toxopeus); 14, Rattan Camp, Snow Mts., 1,150 & 1,200 m. (about 3,750 & 3,900 ft.), Feb.-Mar. 1939 (Toxopeus); 1, Maffin Bay, Aug. 1944 (Darlington); 5, Sansapor (Vogelkop), Aug. 1944 (Darlington); 1, Mt. Nok, Waigeo Is., 2,500 ft., May 1938 (Cheesman). The species probably occurs at low altitudes throughout New Guinea. My specimens were all taken in forest, mostly in piles of dead leaves on the ground or in clumps of living or dead leaves on standing or fallen trees.

Notes. This easily recognized *Colpodes* is the only species of the genus, as here restricted, which is common and widely distributed in the lowlands of New Guinea. It is recorded also from the **Aru** and **Kei Islands** and the northeastern corner of **Australia**, and I have seen specimens from Cape Gloucester, **New Britain** (Darlington) and Malaita, **Solomon Islands** (American Mus.).

COLPODES SAPHYRINUS SLOANEI Maindron

Colpodes papuensis Maindron (nec Sloane) 1908, Nova Guinea **5**, p. 298.
Colpodes sloanei Maindron 1908, Bull. Soc. Ent. France, p. 185.

Description (significant characters only). Very close to the well known Oriental *Colpodes saphyrinus* Chd.; form nearly the same; color similarly purplish-blue. *Head* .79 & .77 width prothorax, formed about as in *saphyrinus*. *Prothorax* subcordate; width/length 1.41 & 1.41; base/apex 1.21 & 1.22; slightly wider and flatter and with relatively slightly wider base than usual in *saphyrinus*; and lateral margins relatively wider. *Elytra* about as in *saphyrinus*; each with a moderate spine at sutural angle; but each elytron at outer angle (outside the subapical sinuation) with a second, shorter, slightly incurving spine rather than an acute tooth as in *saphrinus*. *Lower surface* with prosternal process angulate or subtuberculate at apex in lateral profile but not distinctly margined. *Legs* with hind tarsi a little more slender than in *saphyrinus* but otherwise about same; 4th hind-tarsal segment with long outer and shorter inner lobe; 5th hind-tarsal segment with fine, short, inconspicuous, but nevertheless distinct and regular accessory setae as in *saphyrinus*. *Measurements:* length 13.6–15.1; width 4.7–5.5 mm.

Type. From Cyclops Mts., **Neth. N. G.**; probably in Paris Mus.

Occurrence in New Guinea. **Papua:** 1♂, Kokoda, 1,200 ft., July 1933 (Cheesman); 3♀♀, Dobodura, Mar.–July 1944 (Darlington). **Neth. N. G.**; 1♂, considered a topotype, Mt. Lina, Cyclops Mts., 3,500–4,500 ft., Mar. 1936 (Cheesman); and 8, Rattan Camp, Snow Mts., 1,150 & 1,200 m. (about 3,750 & 3,900 ft.), Feb.–Mar. 1939 (Toxopeus). The specimens from Dobodura were all taken by beating masses of wilting leaves attached to the top of a small fallen tree in heavy forest.

Measured specimens. The ♂ from Kokoda, and 1 ♀ from Dobodura,

Notes. Colpodes saphyrinus and closely related forms at least some of which are perhaps to be considered subspecies (together constituting Jeannel's genus *Nesiocolpodes*, which may be recognizable, though not by the characters given by Jeannel) occur in different areas from the Indo-Chinese Subregion of the Orient through most of the Indo-Australian Archipelago, at least to the Philippines and New Guinea. The New Guinean form, *sloanei*, is best distinguished from the other members of the group by presence of a short spine rather than a mere tooth at the outer angle of each elytron.

Colpodes helluo n. sp.

Description. Form of a large, slender, flattened *Platynus* or of a slender helluonine; piceous or rufo-piceous, appendages a little paler, lateral margins of prothorax and elytra only slightly translucent; surface moderately shining, not iridescent; microsculpture scarcely visible on head and disc of pronotum, more distinct and isodiametric or only slightly transverse in basal foveae and along base and sides of pronotum, still more distinct and only slightly transverse on elytra. *Head* .82 & .81 width prothorax; eyes moderate in size and prominence, with posterior supraocular setae about between their posterior edges; front smooth, with anterior impressions slight; antennae long, normally formed; mentum tooth triangular with vaguely emarginate apex. *Prothorax* more or less cordate; width/length 1.28 & 1.30; base/apex

1.04 & 1.17; sides arcuate anteriorly, strongly sinuate well before basal angles; latter nearly right, but slightly blunted; lateral margins moderately wide and rather strongly reflexed; basal foveae deep, slightly wrinkled but not distinctly punctate; disc normal, impunctate; anterior marginal line distinct and entire, posterior one less well defined but more or less entire. *Elytra* long, almost parallel, depressed; basal margin entire, slightly angulate at humeri; lateral margins moderate; subapical sinuations rather strong; apices bluntly subangulate about opposite 3rd striae, then briefly subtruncate, then strongly spined at sutural angles, the spines a little longer than width of a discal elytral interval; striae very deep, entire, vaguely punctulate; intervals convex, 8th and 9th not much modified toward apex, 3rd with usual 3 dorsal punctures, the anterior one a little farther back than usual. *Lower surface* impunctate or nearly so; abdomen not pubescent; prosternal process normal, simple. *Legs:* hind tarsi slender, with first 4 segments sulcate each side above; 4th hind-tarsal segment shallowly emarginate, not lobed; 5th hind-tarsal segment without obvious accessory setae below. *Male copulatory organs:* Fig. 35. *Measurements:* length 11.6–13.8; width 3.8–4.5 mm.

Types. Holotype ♂ (Leiden Mus.) and 1 ♀ paratype (M.C.Z., No. 28,623) both from Rattan Camp, Snow Mts., **Neth. N. G.**, 1,150 m. (about 3,750 ft.), Feb.–Mar. 1939 (Toxopeus).

Measured specimens. The types.

Notes. Characters for the identification of this species are given in the key, above. In appearance it is unlike any other species of Agonini known to me.

COLPODES LAETUS (Er.)

Anchomenus laetus Erichson 1834 (1835), Nov. Act. Akad. Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum **16**, Suppl. p. 222, Pl. 37, Fig. 2.

Colpodes laetus Andrewes 1930, Cat. Indian Carabidae, p. 123 (see for synonymy and additional references).

Description (significant characters only). Form rather *Platynus*-like; color red, with elytra bright green or blue and with red apices. *Head* .76 & .73 width prothorax. *Prothorax:* width/length 1.31 & 1.30; base/apex 1.25 & 1.22. *Elytra* with outer intervals scarcely modified toward apex. *Legs:* hind tarsi with first 4 segments sulcate each side above; 4th hind-tarsal segment with a moderate outer and shorter inner lobe; 5th hind-tarsal segment without obvious accessory setae. *Male copulatory organs:* Fig. 36. Although it is strikingly colored, the species notably lacks striking or unusual structural characters. *Measurements:* length about 9½–13; width about 3½–4½ mm

Type(s). From Luzon in the **Philippines**; in Zoological Mus., Berlin (seen by Andrewes, 1927).

Occurrence in New Guinea. **Papua:** 4, Dobodura, Mar.–July 1944 (Darlington). **Neth. N. G.:** 1, Hollandia, May 1945 (B. Malkin, U.S.N.M.); 2, Bewani Mts., 400 m. (about 1,300 ft.), July 1937 (W. Stüber, British Mus.); 2, Toem (Maffin Bay), Mar. 1945 (D. B. Vogtman, U.S.N.M.); 5, "Neth. New Guinea" without further locality, "jungle vege.", 225 ft., Oct. 10, 1944 (T. Aarons), Nov. 10, 1944 (T. Aarons), and Dec.–Feb. 1945 (H. A. Levy) (all in American Mus.). The Dobodura specimens were all taken at light.

Measured specimens. One ♂ and 1 ♀ from Dobodura.

Notes. I have seen this species also from Luzon, Leyte, and Mindanao in the **Philippines**; **Celebes** (Andrewes Coll., British Mus.); Bougainville (M.C.Z. & U.S.N.M.) and Kulambangra (British Mus.) in the **Solomons**; and Espiritu Santo, **New Hebrides** (American Mus. and California Acad.).

The coloration of this species is like that of *Euplenes apicalis* (above), but the *Colpodes* is of course much larger (about 9½–13 mm.), with different generic characters (see key to genera, above). It is nearly matched in color also by *Colpodes felix* Andr., known from Buru and the Philippines, but *felix* is much smaller and broader, with different technical characters, probably related to *C. ruficeps*.

C. laetus is a somewhat variable species, but I am not able to divide it into distinct subspecies. In the nine Philippine specimens now before me the elytra are bright green (except of course for the red apices). In most specimens from New Guinea, the Solomons, and the New Hebrides the main elytral color is blue rather than green, but some greenish specimens occur in the New Guinean series. Variation in proportions and in shape of prothorax seems to be more individual than geographical. In some New Guinean specimens the elytra are distinctly denticulate at sutural angles (as usual in the Philippines) but in other New Guinean specimens there is almost no trace of the denticles. Both forms occur in my short series from Dobodura.

COLPODES HABILIS Sl.

Sloane 1907, Deutsche Ent. Zeits., pp. 178 & 179.
Andrewes 1930, Treubia **7**, Suppl., pp. 333 & 338.
van Emden 1937, Stettiner Ent. Zeit. **98**, p. 34.

Description (Significant characters only). A large (about 13–17 mm.) *Colpodes* with greenish, bluish, or purplish elytra which are not spined but denticulate at sutural angles, with outer intervals not much modified toward apex. *Head* .72 & .73 width prothorax. *Prothorax:* width/

length 1.34 & 1.35; base/apex 1.16 & 1.22. *Legs:* hind tarsi slender, with first 4 segments deeply sulcate each side above; 4th hind-tarsal segment with a moderate outer and shorter inner lobe; 5th hind-tarsal segment without obvious accessory setae, but sometimes (perhaps always) with vestigial ones. *Male copulatory organs:* Fig. 37. *Measurements:* length about 13–17; width about 4½–6 mm.

Type. From Sattelberg, **N-E. N. G.**; presumably in Deutsches Entomologisches Institut, Berlin-Dahlem, Germany.

Occurrence in New Guinea. **Papua:** 1, Mafulu, 4,000 ft., Dec. 1933 (Cheesman); 1, Mondo, 5,000 ft., Jan.–Feb. 1934 (Cheesman); 2, Palmer River at Black River, June 7–14, 1936 (Archbold Exp., American Mus.); 1, Mt. Mabiom, July 15, 1936 (Archbold Exp., American Mus.). **N-E. N. G.:** 1, Sattelberg (topotype) (British Mus.). **Neth. N. G.:** 2, Hollandia, 250 ft., Nov. 11, 1944 & May 1945 (H. Hoogstraal, M.C.Z.); 1, same locality, 300–600 m. (about 975–1,950 ft.), Jan. 1938 (W. Stüber, British Mus.); 3, Bewani Mts., 400 m. (about 1,300 ft.), July & Sept. 1937 (W. Stüber, British Mus.); 1, Pukusam Dist. (W. of Tami River), June 1937 (W. Stüber, British Mus.); 1, Mt. Cyclops, 3,500 ft., Mar. 1936 (Cheesman); 21, Araucaria Camp, Snow Mts., 800 m. (about 2,600 ft.), Mar. 1939 (Toxopeus); 24, Rattan Camp, Snow Mts., 1,150 & 1,200 m. (about 3,750 & 3,900 ft.), Feb.–Mar. 1939 (Toxopeus); 1, Sigi Camp, Snow Mts., 1,500 m. (about 4,875 ft.), Feb. 1939 (Toxopeus); 2, Mist Camp, Snow Mts., 1,800 m. (about 5,850 ft.), Jan. & Feb. 3, 1939 (Toxopeus); 10, Mt. Baduri, Japen Is., 1,000 ft., Aug. 1938 (Cheesman); 1, Wasian, Sept. 1939 (R. G. Wind, M.C.Z.); 2, Mt. Nok, Waigeo Is., 2,500 ft., May 1938 (Cheesman).

Measured specimens. One pair (♂ ♀) from Rattan Camp.

Notes. This species is recorded also from **Buru** (Andrewes 1930); I have seen specimens from Cape Gloucester, **New Britain** (Darlington), and from Guadalcanar Is., **Solomons** (J. A. Kusche, Bishop Mus.); and it is recorded also from Vanikoro, **Santa Cruz Islands** (van Emden 1937).

COLPODES BENNIGSENI Sl.

Sloane 1907, Deutsche Ent. Zeits., pp. 177 & 179.
Colpodes louwerensi Andrewes (new synonym).
Andrewes 1937, Bull. Ann. Soc. Ent. Belgique **77**, pp. 39 & 41.
Louwerens 1949, Tijd. v. Ent. **90**, p. 45.

Description (significant characters only). Very large (about 18–21 mm.); color black, elytra with strong purple or green reflections which vary somewhat in different individuals and more in different lights, appendages dark. *Head* .82 & .84 (.81) width prothorax. *Prothorax* rather narrow and narrowly margined; width/length 1.17 & 1.19 (1.19); base/apex 1.09 & 1.11 (1.08) if base measured between posterior-lateral setae, but base actually slightly narrower than apex if measured between apparent (but rounded) basal angles, which are behind the setae; sides moderately arcuate anteriorly, faintly or not distinctly angulate at anterior-lateral setae, nearly straight and rather strongly converging in more than posterior half; anterior and posterior marginal lines entire. *Elytra* rather ample, with weak subapical sinuations, strongly rounded lobes or blunt angulations at apex about opposite 3rd intervals, and denticles at sutural angles; 3rd interval with 3 dorsal punctures but anterior one a little farther forward and others farther backward than normal, the posterior one being very far back, on the declivity; 7th interval toward apex much narrowed but somewhat variable, 8th toward apex compressed to a narrow costa, and 9th narrow and much interrupted by ocellate foveae. *Legs:* hind tarsi with first 4 segments very deeply impressed on each side (and so 3-carinate) above; 4th hind-tarsal segment with a moderate outer and shorter inner lobe; 5th hind-tarsal segment without obvious accessory setae but with minute vestigial ones. *Measurements:* length about 18–21; width about 6½–7¾ mm.

Types. That of *bennigseni* from Sattelberg, **N-E. N. G.**, should be in the Deutsches Entomologisches Institut, Berlin-Dahlem, Germany. That of *louwerensi*, from **Bali**, is in the Andrewes Collection in the British Museum, where I have seen it.

Occurrence in New Guinea. **Papua:** 1, Mafulu, 4,000 ft., Dec. 1933 (Cheesman); 1, Mondo, 5,000 ft., Jan.–Feb. 1934 (Cheesman). **Neth. N. G.:** 2, Humboldt Bay Dist., 1937 (W. Stüber, British Mus.); 1, Bewani Mts., Sept. 1937 (W. Stüber, British Mus.); 1, Pukusam Dist. (W. of Tami River), June 1937 (W. Stüber, British Mus.); 1, Hollandia, Jan.–Mar. 1939 (Toxopeus); 12, Araucaria Camp, Snow Mts., 800 m. (about 2,600 ft.), Mar. 1939 (Toxopeus); 58, Rattan Camp, Snow Mts., 1,150 & 1,200 m. (about 3,750 & 3,900 ft.), Feb.–Mar. 1939 (Toxopeus); 1, Mist Camp, Snow Mts., 1,800 m. (about 5,850 ft.), Jan. 1939 (Toxopeus); 4, Mt. Baduri, Japen Is., 1,000 ft., Aug. 1938 (Cheesman).

Measured specimens. One pair (♂ ♀) from Rattan Camp, and in parentheses a ♀ cotype of *louwerensi* from Bali.

Notes. Outside of New Guinea this species is known from **Bali** (types of *louwerensi*); **Java** (Louwerens 1949); **Celebes** (♂ ♀ received from Louwerens); and Malaita, **Solomon Islands** (1 ♀, American Mus.). I have carefully compared a ♀ cotype of *louwerensi* from Bali with New Guinean specimens of *bennigseni* and find no differences that seem to be of even subspecific value.

COLPODES REX n. sp.

Description. Very large; near average form and convexity for genus; black, pronotum and elytra green or blackish-green or purple-green (varying a little in different individuals but more at different angles), appendages dark; lateral margins of pronotum and elytra invaded by metallic color, not translucent; surface rather shining, not iridescent; microsculpture indistinct on head (but latter with a very little fine, sparse punctulation), light and transverse on pronotum, very fine and transverse on elytra. *Head* .78 & .77 width prothorax; eyes large and prominent, with posterior supraocular setae a little in front of line of posterior edges of eyes; front smooth, with anterior impressions rather shallow and irregular; antennae not very long (in genus), normally formed; mentum tooth triangular. *Prothorax* subhexagonal; width/length 1.31 & 1.24; base/apex 1.05 & .99 if base measured across posterior-lateral setae, but slightly less than .90 if base measured across apparent posterior angles, which are behind the setae; sides slightly arcuate and converging forward anteriorly, subangulate before middle (at anterior-lateral setae), then nearly straight and strongly converging backward, and sometimes slightly sinuate before posterior angles; latter obtuse, narrowly rounded; lateral margins rather narrow especially posteriorly, moderately reflexed; basal foveae not distinct from posterior ends of lateral margins, impunctate; disc with light median and deeper transverse impressions, impunctate; anterior and posterior marginal lines entire, well marked. *Elytra* long, moderately wide, convex, with sides subparallel, only faintly arcuate for most of length; basal margin entire, rounded at humeri; lateral margins narrow; subapical sinuations slight or absent; apices each with a short spine about opposite 3rd stria, then emarginate to denticulate sutural angle; striae fine and light, very finely punctulate, 1st deeper at base and apex, 5th in a depression toward base; intervals flat, scarcely modified toward apex except that 8th tends to overhang 9th at outer posterior curve of elytron; 3rd interval almost normally 3-punctate except posterior puncture farther back than usual, behind apical ¼. *Lower surface* impunctate; abdomen not pubescent; prosternal process simple. *Legs:* posterior tibiae not sulcate along outer edges; posterior tarsi with first 4 segments above lightly but distinctly sulcate on outer side but less distinctly or not sulcate on inner side especially in ♂; 4th hind-tarsal segment rather deeply emarginate but hardly lobed, inner and outer apical angles nearly equal; 5th hind-tarsal segment without obvious accessory setae. *Secondary sexual characters* normal except ♀ usually with 3 (instead of 2) setae each side last ventral segment. *Measurements:* length 19–23; width 6.5–7.7 mm.

Types. Holotype ♂ (British Mus.) and 10 paratypes (British Mus., & M.C.Z., No. 28,624) from Bewani Mts., Humboldt Bay Dist., **Neth. N. G.**, Sept. (some paratypes July) 1937 (W. Stüber). Additional paratypes as follows: **Neth. N. G.:** 1, Pukusam Dist. (W. of Tami R.), June 1937 (W. Stüber, British Mus.); 1, Mt. Cyclops, 3,500 ft., Mar. 1936 (Cheesman); 1, Araucaria Camp, Snow Mts., 800 m. (about 2,600 ft.), Mar. 1939 (Toxopeus); 18, Rattan Camp, Snow Mts., 1,150 & 1,200 m. (about 3,750 & 3,900 ft.), Feb.–Mar. 1939 (Toxopeus); 2, Sigi Camp, Snow Mts., 1,500 m. (about 4,875 ft.), Feb. 22, 1939 (Toxopeus); 20, Mist Camp, Snow Mts., 1,800 m. (about 5,850 ft.), Jan. 1939 (Toxopeus); 1, Top Camp, Snow Mts., 2,100 m. (about 6,825 ft.), Jan. 22, 1939 (Toxopeus); 2, Mt. Baduri, Japen Is., 1,000 ft., Aug. 1938 (Cheesman); 3, Mt. Nok, Waigeo Is., 2,500 ft., May 1938 (Cheesman). **N-E. N. G.:** 1, Wamoro (not located on map) (British Mus., marked "*Colpodes sp. nov.?*" by Andrewes). **Papua:** 1, Mafulu, 4,000 ft., Dec. 1933 (Cheesman); 4, Fly R. 5 mi. below Palmer R., May 14–31, 1936 (Archbold Exp., American Mus.); 1, Palmer R. at Black R., June 15–22, 1936 (Archbold Exp., American Mus.); 1, Mt. Mabiom, July 15, 1936 (Archbold Exp., American Mus.). The records suggest that this is a species of the lower and middle mountain slopes, and that it commonly extends to higher altitudes than *habilis* or *bennigseni.*

Measured specimens. The ♂ holotype and 1 ♀ paratype from the Bewani Mts.

Notes. This magnificent species is apparently related to the preceding (*bennigseni*), which it resembles in large size and striking appearance and in at least two significant technical characters: the position of the apparent posterior angles of the prothorax (behind the posterior-lateral setae) and the position of the posterior punctures of the 3rd elytral intervals (unusually far back, though not so far back as in *bennigseni*). However *rex* differs from *bennigseni* not only in such specific characters as presence of metallic color on pronotum as well as elytra, relatively narrower head, more hexagonal prothorax, finer elytral striae, and presence of apical elytral spines, but in certain other characters which are surprising if the species are really closely related. For example, the outer elytral intervals especially near apex are strongly compressed in *bennigseni* but not in *rex;* and the hind tarsi are strongly sulcate on both sides above in *bennigseni* but only lightly so or sometimes not distinctly sulcate at all on the inner side in *rex.*

COLPODES ANTEDENS n. sp.

Description. Form almost of *Agonum* (*s. s.*) but larger, more elongate, with relatively longer head and spined elytra; black, appendages dark; lateral margins of prothorax and elytra vaguely or not translucent; surface moderately shining, not iridescent; microsculpture of head faint, nearly isodiametric; of pronotum faint; of elytra more distinct, of rather large, only slightly transverse meshes. *Head* .70 width prothorax; eyes moderately large and prominent; genae short, oblique, not prominent; posterior supraocular setae about between posterior edges of eyes; front smooth, impressed on each side anteriorly; antennae rather long and slender, normally formed; mentum tooth narrowly triangular with slightly blunted apex. *Prothorax:* width/length 1.40; base/apex 1.21; sides evenly arcuate for most of length, almost straight and converging before basal angles; latter obtuse but only slightly blunted; lateral margins rather wide and rather strongly reflexed; basal foveae deep, vaguely roughened or subpunctate; disc with usual impressions, impunctate; anterior and posterior marginal lines entire. *Elytra* rather long, normally convex, with sides only slightly arcuate for most of length; basal margin entire, obtusely angulate at humeri; lateral margins moderate; outer angles distinct, almost right; subapical sinuations emarginate; apices spined opposite ends of 3rd intervals, then obliquely emarginate to slightly obtuse (nearly right) sutural angles; spines slightly longer than width of 1 discal interval; striae moderately deep, finely punctulate; intervals convex, 8th and 9th not much modified toward apex; 3rd normally 3-punctate. *Lower surface* impunctate; abdomen not pubescent; prosternal process simple. *Legs:* hind tibiae not sulcate along outer edges; hind tarsi slender, lightly sulcate each side above; 4th hind-tarsal segment deeply emarginate, outer and inner angles prominent, about equal; 5th hind-tarsal segment with short and inconspicuous but distinct accessory setae below. *Male copulatory organs* as figured (Fig. 38). *Measurements:* length 16.6; width about 6 mm.

Type. Holotype ♂ (British Mus.) from Mt. Lina, Cyclops Mts., **Neth. N. G.**, 3,500 ft., Mar. 1936 (Cheesman); unique.

Measured specimen. The type.

Notes. This species should be easily recognized by characters given in the key to species of *Colpodes*, above. It resembles the following ones (*acuticauda, sinuicauda, simplicicauda*) in being rather large and black, but I am not sure it is really related to any of them, nor am I sure that the latter are related among themselves. It (*antedens*) is notable not only for having the outer angles of the elytra well defined, but also for possessing distinct, though very small, accessory setae on the 5th hind-tarsal segments.

Colpodes acuticauda n. sp.

Description. Large; black, appendages black or piceous; surface rather dull, faintly silky but not iridescent; microsculpture fine but distinct, isodiametric on head, only slightly transverse on pronotum and elytra; upper surface also faintly, sparsely punctulate. *Head* .76 & .77 width prothorax; eyes smaller than usual in genus but prominent; genae angulately prominent in profile; posterior supraocular setae about between posterior edges of eyes; vertex transversly impressed; front a little irregular, with very slight anterior impressions; antennae of moderate length, normally formed; mentum tooth triangular, with apex rounded. *Prothorax:* width/length 1.38 & 1.44; base/apex 1.07 & 1.06; sides arcuate for most of length, variably sinuate before somewhat obtuse but well defined posterior angles; lateral margins moderate, rather strongly reflexed especially posteriorly; basal foveae moderate or rather shallow, not punctate; disc less convex than usual, impunctate; anterior and posterior marginal lines vague or obsolete. *Elytra* of about normal proportions, slightly more convex than usual; sides subparallel for much of length; basal margin incomplete, obliterated inwardly from bases of 5th or 4th striae; lateral margins rather narrow; outer angles not defined; subapical sinuations almost absent; apices strongly angulate opposite 2nd intervals, with angles usually slightly produced into acute denticles; sutural angles not defined (unless the aforementioned angulations are sutural angles displaced outward); striae rather deep, impunctate; intervals moderately convex, 8th narrowed and longitudinally impressed toward apex, 9th widened and irregular toward apex; 3rd interval with only 1 dorsal puncture, far back, at top of declivity. *Lower surface* impunctate; abdomen with a little fine pubescence irregularly distributed; prosternal process simple. *Legs:* posterior tibiae not sulcate along outer edges; posterior tarsi slender, sulcate each side above; 4th hind-tarsal segment deeply emarginate, outer angle forming a very short lobe, slightly longer than inner one; 5th hind-tarsal segment without obvious accessory setae below. *Male copulatory organs:* Fig. 39. *Measurements:* length 17.6–18.3; width about 6 or slightly more mm.

Types. Holotype ♀ (British Mus.) and 1 ♀ paratype (M.C.Z., No. 28,625) from Mt. Tafa, **Papua**, 8,500 ft., Mar. 1934 (Cheesman); and 1 ♂ paratype from Top Camp, Snow Mts., **Neth. N. G.**, 2,100 m. (about 6,825 ft.), Jan. 22, 1939 (Toxopeus).

Measured specimens. The ♀ holotype and ♂ paratype.

Notes. This very distinct new species has several characters (form of eyes and genae, reduction of basal margin of elytra, reduction of dorsal punctures of elytra, dullness of surface) which suggest that it may be near the ancestral stock of *Idiagonum* (new genus described below), but it is still much more of a *Colpodes* than an *Idiagonum*, with eyes still only a little modified, one dorsal elytral puncture still remaining, no added 10th elytral interval, no setae on prosternal process, and fully developed inner wings.

COLPODES SINUICAUDA n. sp.

Description. Rather large; black, appendages dark, lateral margins of prothorax slightly and of elytra scarcely translucent; surface moderately shining, not iridescent; microsculpture rather light, isodiametric on head, transverse on pronotum, very fine and transverse on elytra. *Head* .79 & .79 width prothorax; eyes much smaller and somewhat less prominent than usual in genus; genae long, oblique, nearly straight but with a slight sinuation (in profile) posteriorly; posterior supraocular setae a little behind line of posterior edges of eyes; front nearly smooth, a little irregular and slightly impressed each side anteriorly; antennae moderately long, normally formed; mentum tooth absent in both specimens. *Prothorax:* width/length 1.33 & 1.43; base/apex 1.06 & 1.06; sides moderately or strongly arcuate for much of length, strongly sinuate well before slightly acute basal angles; lateral margins moderate, moderately reflexed; basal foveae average, impunctate; disc normal, impunctate; anterior and posterior marginal lines present but vague. *Elytra* of normal proportions, normally convex, with sides slightly arcuate; basal margin entire, faintly angulate at humeri; lateral margins moderately wide; outer angles not defined; subapical sinuations strong; apices strongly rounded or subangulate about opposite 3rd intervals, then subtruncate to more or less plainly denticulate sutural angles; striae well impressed, not distinctly punctulate; intervals slightly convex, 8th and 9th not much modified toward apex; 3rd interval normally 3-punctate. *Lower surface* nearly impunctate, but abdomen with a little fine scattered punctation (apparently without pubescence) especially on segments 3 & 4; prosternal process simple. *Legs:* posterior tibiae not sulcate along outer edges; posterior tarsi apparently stouter in ♂ than in ♀, not distinctly sulcate above; 4th hind-tarsal segment with rather long outer and shorter inner lobe; 5th hind-tarsal segment without obvious accessory setae below. *Male copulatory organs:* Fig. 40. *Measurements:* length 13.6–14.8; width 4.8–5.3 mm.

Types. Holotype ♂ (Leiden Mus.) from Sigi Camp, Snow Mts., **Neth. N. G.**, 1,500 m. (about 4,875 ft.), Feb. 24, 1939 (Toxopeus); and 1 ♀ paratype (M.C.Z., No. 28,626) from Lower Mist Camp, Snow Mts., 1,700 m. (about 5,525 ft.), Jan. 17, 1939 (Toxopeus).

Measured specimens. The types.

Notes. Besides the key characters, which are distinctive enough, this species possesses one characteristic which, so far as I know, is unique in *Colpodes* even in the broadest sense: absence of the usual mentum tooth. However, I do not want to stress this too much. The tooth may possibly be broken off, although that this should have happened in the same way in both specimens seems unlikely.

COLPODES SIMPLICICAUDA n. sp.

Description. Very large; black, appendages dark, lateral margins of prothorax and elytra vaguely or not translucent; surface moderately shining, not iridescent; microsculpture indistinct on head, light and moderately transverse on pronotum, heavier but only moderately transverse on elytra; surface of head, pronotum, and elytra also with very fine, sparse, inconspicuous punctulation. *Head* .81 & .79 width prothorax; eyes much smaller and less prominent than usual in genus; genae long, oblique, slightly sinuate in profile (transversely swollen in side view) posteriorly; posterior supraocular setae slightly behind line of posterior edges of eyes; head rather deeply transversely impressed posteriorly; front slightly, irregularly wrinkled and very slightly impressed each side anteriorly; antennae moderately long, normally formed; mentum tooth triangular with apex blunted or vaguely emarginate. *Prothorax:* width/length 1.31 & 1.37; base/apex .96 & 1.02; sides moderately or weakly arcuate for much of length, broadly or moderately sinuate before nearly right, well formed basal angles; lateral margins moderately wide, normally reflexed; basal foveae normal, impunctate; disc normal, slightly and superficially transversely wrinkled, impunctate (except for fine, sparse punctulation mentioned above); anterior and posterior marginal lines entire, well impressed. *Elytra* rather long, of normal width and convexity, nearly parallel-sided; basal margin entire, not distinctly angulate at humeri; lateral margins rather narrow; outer angles not defined; subapical sinuations weak; apices nearly conjointly rounded, with sutural angles slightly dehiscent, not denticulate; striae moderately impressed, not distinctly punctate; intervals slightly convex, 8th rather strongly narrowed and more convex toward apex and 9th slightly widened toward apex (but these intervals still not very much modified toward apex); 3rd interval normally 3-punctate, but posterior puncture rather far back, at top of declivity. *Lower surface* impunctate; abdomen not pubescent; prosternal process normal. *Legs:* posterior tibiae not or vaguely sulcate along outer edges; posterior tarsi rather lightly sulcate each side above (inner sulcus sometimes almost obliterated, especially in ♂); 4th hind-tarsal segment with rather long outer and shorter inner lobe; 5th hind-tarsal segment without obvious accessory setae below. *Measurements:* length about 17–21; width 5.7–7.0 mm.

Types. Holotype ♂ (Leiden Mus.) and 1 ♂ paratype (M.C.Z., No. 28,627) from Ibele (Iebele) Camp, Snow Mts., **Neth. N. G.**, 2,250 m. (about 7,325 ft.), Nov.–Dec. 1938 (Toxopeus); 5 paratypes (all ♀ ♀) from Mist Camp, Snow Mts., 1,800 m. (about 5,850 ft.), various dates in Jan. 1939 (Toxopeus); 1 ♀ paratype from Sigi Camp, Snow Mts., 1,500 m. (about 4,875 ft.), Feb. 17, 1939 (Toxopeus); and 1 ♀ paratype from Saiko (Bubu R., Upper Waria R.), **N-E. N. G.**, 5,500–6,000 ft., Sept.–Oct. 1936 (F. Shaw-Mayer, British Mus.).

Measured specimens. The ♂ holotype, and 1 ♀ paratype from Mist Camp.

Notes. This species should be easily identifiable by characters given in the key to species of *Colpodes*, above. It lacks the conspicuous or unusual structural peculiarities which define, in different ways, the three preceding species.

PLICAGONUM new genus

Diagnosis. See key to genera.

Description. Rather large (14.3–18.5 mm.), somewhat *Platynus*-like (Fig. 3), brownish forms with fully developed wings and all usual supraocular and pronotal setae; surface above virtually impunctate except for fine punctulation on head and pronotum; microsculpture absent on head, almost absent on pronotum, rather fine but deeply impressed and not or only slightly transverse on elytra. *Head* only moderately elongate, with large prominent eyes; posterior supraocular setae at or in front of line of posterior edges of eyes; front strongly but irregularly longitudinally wrinkled between eyes; anterior frontal impressions slight; antennae rather slender, normal in structure; mentum tooth triangular with apex more or less (irregularly) blunted. *Prothorax* normal. *Elytra* margined at base; fully striate; 3rd interval normally 3-punctate except anterior puncture missing on one or both sides in several individuals: 8th & 9th intervals not much modified toward apex; subapical sinuations weak; apices variable as described in species. *Inner wings* fully developed. *Lower surface* virtually impunctate; abdomen not pubescent; prosternal process normal. *Legs* normally formed; hind tibiae not sulcate along outer edges; hind tarsi slender, sulcate each side above (but sulci, especially inner one, sometimes faint); 4th hind-tarsal segment deeply emarginate, with short lobes, outer one scarcely longer than inner; 5th hind-tarsal segment without obvious accessory setae; claws simple; sole clothed with numerous setae not in regular rows but with middle of sole narrowly bare. *Secondary sexual characters* normal. *Male copulatory organs* as figured (Figs. 41 & 42).

Genotype. Plicagonum fulvum n. sp. (below).

Generic distribution. Mountains of New Guinea.

Notes. This genus, though not very different from *Colpodes* even as here restricted and perhaps actually of only subgeneric value, is distinguished especially by the longitudinal wrinkling of the head, and is a natural group which has undergone more or less radiation at rather high altitudes in New Guinea. I here describe only two forms of the genus, but my few scattered specimens of *rugifrons* are so variable as to suggest that this species will be found to break up into distinct subspecies on different mountain ranges.

Key to the Species of Plicagonum

Elytral apices spined or at least acutely angulate about opposite 3rd intervals (p. 174) . . . . *rugifrons*

Elytral apices neither spined nor acutely angulate opposite 3rd intervals (p. 175) . . . . *fulvum*

PLICAGONUM RUGIFRONS n. sp.

Description. With characters of genus as described above. Brownish-piceous, elytra usually (not always) browner with piceous apices and sometimes faintly striped (with striae piceous and middles of intervals brown), appendages brown, lateral margins of prothorax moderately translucent. *Head* .72 & .73 width prothorax. *Prothorax:* width/length 1.40 & 1.40; base/apex 1.22 & 1.20; sides variably arcuate anteriorly, nearly straight and converging and sometimes faintly sinuate posteriorly; basal angles moderately to very obtuse; lateral margins rather wide but only slightly reflexed (a little more so toward base); basal foveae rather small but deep, sometimes slightly wrinkled but not punctate; disc with very light median longitudinal line and deep anterior and posterior transverse impressions, impunctate; anterior and posterior marginal lines entire, deeply impressed. *Elytra* rather ample, more convex than usual in *Colpodes,* nearly parallel-sided (slightly narrowed anteriorly); basal margin rounded or faintly angulate at humeri; lateral margins narrow; apices each with an acute tooth or short spine opposite 3rd interval, then emarginate to sutural angle; latter vaguely or distinctly denticulate; striae not deeply impressed, not distinctly punctulate; intervals nearly flat to slightly convex. *Male copulatory organs:* Fig. 41. *Measurements:* length about 17.5–18.5; width 6.1–6.4 mm.

Types. Holotype ♂ (Leiden Mus.) and 2 ♀♀ paratypes (1 in M.C.Z., No. 28,628) all from Top Camp, Snow Mts., **Neth. N. G.**, 2,100 m. (about 6,825 ft.), Jan. 22 (type), Jan. 26, & Feb. 2, 1939 (Toxopeus).

Other material. One ♀, Mt. Misim, Morobe Dist., **N-E. N. G.** (Stevens, M.C.Z.); and 1 ♀, Mt. Tafa, **Papua**, 8,500 ft., Mar. 1934 (Cheesman).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This species is defined and discussed in the key and under the generic description, above.

PLICAGONUM FULVUM n. sp.

Description. With characters of genus as described above. Form as figured (Fig. 3); brownish- or reddish-piceous, elytra typically rather pale-brown with darker apices and sometimes also with stripes along striae slightly darker (Moss Forest Camp specimens have elytra less contrastingly pale); appendages light-brown; lateral margins of prothorax broadly translucent. *Head* .76 & .79 width prothorax; front in types a little less wrinkled especially at middle than in *rugifrons* (but strongly wrinkled in Moss Forest Camp specimens of *fulvum*). *Prothorax:* width/length 1.35 & 1.38; base/apex 1.14 & 1.22; sides moderately arcuate anteriorly, nearly straight and converging and usually slightly sinuate posteriorly; otherwise as in *rugifrons*. *Elytra* as in *rugifrons* except apices only more or less rounded-prominent about opposite 3rd intervals, then obliquely subtruncate or slightly emarginate to vaguely or not denticulate sutural angles. *Male copulatory organs* as figured (Fig. 42). *Measurements:* length (types) 14.3–15.6; width (types) 5.1–5.8 mm. (Moss Forest Camp specimens about 18.5 mm. long).

Types. Holotype ♂ (Leiden Mus.) and 9 paratypes (some in M.C.Z., No. 28,629) from Top Camp, Snow Mts., **Neth. N. G.**, 2,100 m. (about 6,825 ft.), Jan. 20–Feb. 8 (holotype Jan. 22), 1939 (Toxopeus).

Other material. Two, referred to in description above, from Moss Forest Camp, Snow Mts., 2,800 m. (about 9,100 ft.), Oct. 9–Nov. 5, 1938 (Toxopeus).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. Sufficiently characterized in the key to species, above. The Moss Forest specimens may represent a different subspecies or species, but more material is needed to prove it.

LITHAGONUM new genus

Diagnosis. Generally similar to *Notagonum* (of which see description) except in the following characters. Posterior-lateral setae of pronotum absent. Much of upper surface of head and pronotum, elytral striae, and much of lower surface rather closely and more or less coarsely punctate; upper surface without reticulate microsculpture except (in some forms only) at sides and apices of elytra. Male usually with 2 or more (not 1) and ♀ usually with 4 or more (not 2) setae each side last ventral segment.

Description. See that of single species, below.

Genotype. Lithagonum annulicorne dilutior n. subsp., below.

Generic distribution. Much or all of New Guinea in suitable habitats.

Notes. The single species of this genus, with five subspecies, is more fully described below. It is perhaps derived from *Notagonum.* It is somewhat similar superficially to *Notagonum subnigrum* Darl., which it somewhat resembles in habits too, but in my experience *Lithagonum* is even more strictly confined to cobble-stone and similar areas on the banks and bars of rather large streams. Different populations of *Lithagonum* are probably more or less isolated from each other by this habitat restriction, and this may account for the existence of the several distinct subspecies here described.

LITHAGONUM ANNULICORNE (Maindr.)

Colpodes annulicornis Maindron 1908, Nova Guinea **5**, p. 297.
Ibid. 1908, Bull. Soc. Ent. France, p. 185.

Description (species as a whole). Form (Fig. 4) rather *Platynus*-like, but head relatively large, prothorax rather small-cordate, and elytra rather wide and convex; black, appendages brown or piceous; upper surface extensively punctate, but polished between the punctures, without reticulate microsculpture except sometimes at sides and apices of elytra. *Head:* relative widths given under subspecies; eyes rather large and prominent; both pairs of supraocular setae present, posterior ones about between posterior edges of eyes; front normally convex, with rather deep anterior impressions; surface rather closely punctate especially across base and at sides, with middle of front much less or not punctate; antennae rather long and slender, normal in structural details; mentum tooth triangular, more or bless blunted at apex. *Prothorax* narrowly cordate; proportions given under subspecies; sides arcuate anteriorly, strongly sinuate well before right or acute basal angles; lateral margins narrow, with usual anterior-lateral setae about

$2/5$ from apex but no posterior-lateral ones; basal foveae small, shallow, sometimes more or less linear, rugosely punctate, and areas between and before them also more or less closely punctate; disc with median area less closely or not punctate, with usual median and slight transverse impressions; basal and apical marginal lines poorly defined or absent. *Elytra* rather broad and convex, varying in length in different subspecies; sides subparallel (often slightly arcuate) at middle; humeri broadly rounded; base margined, margin usually slightly angulate at humeri; lateral margins moderate; subapical sinuations moderate, broad, each ending in a prominent angulation, tooth, or short spine about opposite 4th interval, then subtruncate or more or less deeply emarginate to sutural angle; latter usually (not always) more or less denticulate; striae deep, entire except some very slightly abbreviated at base, more or less coarsely punctate; intervals convex, 8th and 9th not much modified toward apex; 3rd interval normally 3-punctate. *Inner wings* fully developed. *Lower surface* with all sterna and base of abdomen closely and more or less coarsely punctate; abdomen variable (slightly to extensively), rather sparsely pubescent; prosternal process simple. *Legs:* hind tibiae not sulcate along outer edges; hind tarsi slender, lightly or not distinctly sulcate each side above; 4th hind-tarsal segment deeply emarginate, with short outer lobe and subequal or slightly shorter inner one; 5th hind-tarsal segment without obvious accessory setae; claws simple. *Secondary sexual characters* normal except ♂ with usually 2, ♀ with usually about 4 setae each side last ventral segment. *Male copulatory organs* as figured (for subsp. *dilutior*, Fig. 43). *Measurements:* see under subspecies.

Types. From "Tana Mera", "Jamur supérieur", and "Moso", **Neth. N. G.**; 4 examples in all, probably now in Paris Mus. I here restrict the type locality to the first one named, commonly spelled Tanahmerah (Bay), on the north coast at the west end of the Cyclops Mts. (Moso is just east of the Tami River, which is not far east of the Cyclops Mts. "Jamur supérieur" is probably far to the west, in the vicinity of Lake Jamur.)

Occurrence in New Guinea. See under subspecies.

Measured specimens. See under subspecies.

Notes. It should be noted that, although the exact form of the elytral apices varies in different subspecies, it varies somewhat also in individuals from single localities. It should not be used as a subspecific character except after examination of series. The habitat of this species has been described under the genus, above.

After the preceding discussion of types was written, I have examined one apparent cotype of *annulicorne*, sent by the Paris Museum. Unfortunately the locality of this specimen is not clear, but it appears to be "B. Jamoer", and the date of collection is 5.VIII.1903. This may be the cotype originally recorded from "Jamur supérieur". In its characters (elytra with 9th intervals not reticulate and apices with relatively well developed spines opposite 3rd intervals and relatively short sutural denticles) this specimen agrees better with *politior* than with any other form here recognized, but it may well be a different, undescribed subspecies. However this may be, I see no reason now to change the arrangement of subspecies proposed below.

Key to Subspecies of Lithagonum annulicorne (Maindr.)

1. Legs brown; (at least 9th and usually also 8th elytral intervals with distinct reticulate microsculpture); (Papua); (p. 178) . . . . *dilutior*
– Legs darker, piceous 2
2. No reticulate microsculpture (or rarely faint traces of it) even on 9th intervals at middle of length; (N-E. N. G.) 3
– At least 9th intervals of elytra (and often also 8th etc.) with distinct reticulate microsculpture; (Neth. N. G.) 4
3. Stouter; apices of elytra with relatively prominent denticles or short spines; (Markham Valley & vic.) (p. 179) . . . . *politior*
– More slender; apices of elytra with less prominent denticles; (Bismarck Range) (p. 179) . . . . *bismarckense*
4. Stouter; elytral apices with outer denticles more prominent; elytral striae coarsely punctate; (Cyclops Mts. & vic.) (p. 180) . . . . . . *annulicorne s. s.*
– More slender and depressed; elytral apices with outer denticles usually less prominent (but variable); elytral striae more finely punctate; (vic. of Snow Mts.) (p. 180) . . . . *baliem*

LITHAGONUM ANNULICORNE DILUTIOR n. subsp.

Description. Form as figured (Fig. 4). Smaller than other subspecies. Legs brown (not blackish). *Head* .90 & .87 width prothorax. *Prothorax:* width/length 1.20 & 1.22; base/apex 1.03 & 1.03. *Elytra* relatively short (in species) and usually a little more oval (with more arcuate sides) than in other subspecies; apices variable, usually comparatively weakly emarginate between denticles, and latter usually comparatively small, with outer ones often no more prominent than sutural ones (but in some individuals outer ones are slightly or much more prominent than sutural ones); striae moderately coarsely punctate; at least 9th, almost always 8th, and sometimes less distinctly 7th etc. intervals with somewhat irregular, somewhat transverse reticulate microsculpture (microsculpture almost lacking on 8th though distinct on 9th intervals in one individual from Kokoda). *Male copulatory organs* as shown in Fig. 43. *Measurements:* length 8.0–9.1; width 3.1–3.5 mm.

Types. Holotype ♂ (M.C.Z. No. 28,630) and 21 paratypes from Dobodura, **Papua**, Mar.–July 1944 (Darlington). Additional paratypes from **Papua** as follows: 4, (near) Oro Bay, Dec. 1943 (Darlington); 31, Kokoda, 1,200 ft., Aug. 1933 (Cheesman). These three localities are within about 40 miles of each other, all on north-flowing drainage systems.

Measured specimens. The ♂ holotype and 1 ♀ paratype from Dobodura.

LITHAGONUM ANNULICORNE POLITIOR n. subsp.

Description. Legs blackish. *Head* .83 & .84 width prothorax. *Prothorax:* width/length 1.18 & 1.17; base/apex 1.06 & .98. *Elytra* relatively short, slightly suboval (with sides slightly, variably arcuate); apices rather strongly emarginate between denticles, and outer denticles usually (not always) much more prominent than sutural ones; striae moderately coarsely punctate; all intervals including 8th and 9th without reticulate microsculpture at least at middle of length (1 specimen from Nadzab has 9th intervals faintly reticulate). *Measurements:* length 9.1–10.2; width 3.4–4.0 mm.

Types. Holotype ♂ (M.C.Z. No. 28,631) and 20 paratypes from Nadzab, lower Markham Valley, **N-E. N. G.**, July 1944 (Darlington); and 4 paratypes from Lae, also in the lower Markham Valley, Oct. 1944 (Darlington).

Other material. Eighteen, Morobe Dist., **N-E. N. G.** (some specifically from Surprise Creek, Sept. 28 & Oct. 7) (Stevens, M.C.Z.) The Morobe Dist. is not far south of the Markham Valley.

Measured specimens. The ♂ holotype and 1 ♀ paratype from Nadzab.

LITHAGONUM ANNULICORNE BISMARCKENSE n. subsp.

Description. Legs blackish. *Head* .90 & .86 width prothorax. *Prothorax:* width/length 1.20 & 1.18; base/apex 1.01 & 1.02. *Elytra* slightly more elongate, less oval, and less convex than in preceding (*politior*); apices comparatively weakly emarginate between denticles, and latter less prominent than in *politior*; striae comparatively less coarsely punctate; all intervals including 8th and 9th without reticulate microsculpture at least at middle of length (except 9th intervals faintly reticulate in 1 specimen). *Measurements:* length 9.3–10.1; width 3.5–3.8 mm.

Types. Holotype ♂ (M.C.Z. No. 28,632) and 7 paratypes from

Chimbu Valley, Bismarck Range, **N-E. N. G.**, 5,000–7,500 ft. (probably all actually from near 5,000 ft.), Oct. 1944 (Darlington).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

LITHAGONUM ANNULICORNE ANNULICORNE (Maindr.)

For references, see species as a whole, above.

Description. Legs blackish. *Head* .86 & .87 width prothorax. *Prothorax:* width/length 1.20 & 1.17; base/apex 1.00 & 1.01. *Elytra* relatively short, convex, subquadrate (with sides at most very slightly arcuate at middle); apices rather deeply emarginate between denticles; outer denticles large, almost short spines, much more prominent than sutural denticles; striae coarsely punctate; 9th and (much less distinctly) 8th intervals with reticulate microsculpture. *Measurements:* length 9.6–9.8; width about 3.7 mm.

Types. As indicated under species as a whole, where type locality is restricted to "Tana Mera" (Tanahmerah Bay), at western end of Cyclops Mts., **Neth. N. G.**

Occurrence in New Guinea. I have seen only 3 ♀♀ referable to typical *annulicorne*, all taken not far from the type locality, at Sabron, Cyclops Mts., 930 ft., Apr. 1936 (Cheesman).

Measured specimens. Two of the 3 ♀♀ recorded above.

Notes. The present description covers only the subspecific characters of typical *annulicorne.* The species as a whole is more fully described above.

LITHAGONUM ANNULICORNE BALIEM n. subsp.

Description. Legs blackish. *Head* .90 & .94 width prothorax. *Prothorax:* width/length 1.29 & 1.23; base/apex 1.01 & .98. *Elytra* relatively longer than in typical *annulicorne* and less convex; apices usually less emarginate between denticles, and outer denticles smaller and less prominent than in *annulicorne s. s.*; striae less coarsely punctate than in other subspecies; reticulate microsculpture always distinct on 9th, usually so on 8th, and often faintly visible on discal intervals too. *Measurements:* length 9.3–10.0; width about 3.3–3.7 mm.

Types. Holotype ♂ (Leiden Mus.) and 12 paratypes (some in M.C.Z., No. 28,633) all from Baliem Camp, Snow Mts., **Neth. N. G.**, 1,700 m. (about 5,525 ft.), Nov. 16–27, 1938 (Toxopeus).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

IRIDAGONUM new genus

Diagnosis. Small or medium sized (8.2–13.4 mm.); *Agonum*-like or rarely fusiform; wing-and-seta formula +w, (+)+, −+, (+)++; elytra always strongly iridescent, characteristically toothed at sutural angles but not otherwise armed, usually with 7th and 8th intervals longitudinally impressed toward apex (not so in *quadripunctellum*); sides of body below always more or less strongly punctate.

Description. *Agonum*-like or fusiform; color including that of appendages always dark; upper surface always strongly iridescent especially on elytra, impunctate except sometimes punctate in basal foveae of pronotum; microsculpture light or very fine, not distinguishable at 54X except sometimes on front of head. *Head* only moderately elongate; eyes moderate in size, varying in prominence; both pairs supraocular setae present except anterior pair absent in *subfusum;* posterior pair between or behind line of posterior edges of eyes; antennae of average or less than average length, normally formed; frontal impressions slight; mentum tooth triangular, more or less blunted at tip. *Prothorax* with anterior-lateral setae always absent, posterior-lateral ones always present; otherwise differing in details in different species. *Elytra* margined at base, the margin always strongly (obtusely to about rectangularly) angulate at humeri; subapical sinuations always slight or absent; sutural angles always with denticles or short spines but apices not otherwise armed; striae normal; 7th and 8th intervals and sometimes others at least toward apex deeply longitudinally impressed and so appearing doubled (except not so in *quadripunctellum*). *Inner wings* fully developed. *Lower surface* with sides of sterna extensively and more or less closely but irregularly punctate; abdomen not pubescent; prosternal process normal. *Legs* normally formed, as in *Notagonum*, but 4th hind-tarsal segment always simply emarginate, not distinctly lobed, and 5th hind-tarsal segment always with fine, short, but distinct accessory setae; claws simple. *Secondary sexual characters* normal. *Male copulatory organs* as figured (Figs. 44 & 45).

Genotype. *Iridagonum quadripunctum* n. sp. (below).

Generic distribution. Widely distributed in New Guinea; as yet unknown elsewhere.

Notes. The species of this new genus form a natural group apparently endemic to New Guinea, perhaps derived from *Notagonum.* Two of the species (*quadripunctum* and *sexpunctum*) are unusually variable in form and proportions, but after careful study I can distinguish no more than the four species keyed out below. I have taken only one species (*quadripunctum*) of this genus in its natural habitat, among dead leaves on the ground in heavy rainforest. This is probably the habitat of the other species too. The types of *quadripunctellum* were found in flood-debris in forested or formerly forested country. Most of the specimens of *quadripunctum* and *sexpunctum* collected by Cheesman and Toxopeus were apparently caught in light traps, for the specimens are liberally sprinkled with scales of Lepidoptera.

Key to the Species of Iridagonum

1. Third interval of elytron 2-punctate (anterior puncture missing); (form rather *Agonum*-like) 2
– Third interval 3-punctate 3
2. Larger (9.3–13.4 mm.); elytral intervals 7 & 8 deeply longitudinally impressed at least toward apex (p. 182) . . . . *quadripunctum*
– Smaller (8.2–9.0 mm.); elytral intervals not or only slightly impressed (p. 183) . . . . *quadripunctellum*
3. Form *Agonum*-like; both pairs of supraocular setae present (p. 184) . . . . . . *sexpunctum*
– Form fusiform; anterior supraocular setae missing (and eyes smaller and more abrupt than usual) (p. 185) . . . . *subfusum*

IRIDAGONUM QUADRIPUNCTUM n. sp.

Description. With characters of genus as described above. Form of broad *Agonum s. s.* (Fig. 5). *Head* .67, .67, & .69 width prothorax; eyes normally formed, of moderate size and prominence; both pairs supraocular setae present, posterior ones about between posterior edges of eyes. *Prothorax* moderately narrowed behind and somewhat more so in front; width/length 1.40, 1.33, & 1.36; base/apex 1.28, 1.25, & 1.26; anterior angles only moderately prominent; sides rather broadly arcuate anteriorly, nearly straight (or slightly arcuate or slightly sinuate in some individuals) and moderately converging posteriorly; posterior angles obtuse, narrowly rounded; lateral margins moderate, wider posteriorly, not sharply defined, only moderately reflexed; basal foveae rather broad and shallow, variably (usually rather closely) punctate; disc with median line moderately impressed, transverse impressions slight, anterior marginal line light and variable, posterior one still lighter, often absent. *Elytra* rather short and broad, somewhat variable in form, slightly and variably impressed before middle; basal margin strongly but obtusely angulate or subangulate at humeri; striae moderately impressed, faintly or not punctulate; 7th interval apically, 8th for much of length, (and 9th somewhat variably) longitudinally impressed; 3rd interval 2-punctate (anterior puncture missing); sutural angles with short, slightly out-curving spines in large individuals but with only strong denticles in smaller individuals. *Male copulatory organs* as figured (Fig. 44). *Measurements:* length 9.3–13.4; width 3.8–5.0 mm.

Types. Holotype large ♂ (M.C.Z. No. 28,634) and 10 paratypes (including entire size-range of species) from Dobodura, **Papua,** Mar.–July 1944 (Darlington). Also the following additional paratypes: **Papua:** 1, Kokoda, 1,200 ft., Aug. 1933 (Cheesman); 1, Mafulu, 4,000 ft., Dec. 1933 (Cheesman); 2, Palmer River at Black River, June 7–14 & 15–22, 1936 (Archbold Exp., American Mus.). **N-E. N. G.:** 1, Sattelberg (British Mus.); 3, Aitape, Aug. 1944 (Darlington). **Neth. N. G.:** 1, Dorey ("Dory") (Vogelkop) (British Mus.); 1, mountain slope above Bernhard Camp, Snow Mts., 100 m. (about 325 ft.), Apr. 1939 (Toxopeus); 1, Rattan Camp, Snow Mts., 1,150 m. (about 3,750 ft.), Feb.–Mar. 1939 (Toxopeus).

Other material. Four, Waigeo Is., **Neth. N. G.**, (Mt. Nok, 2,500 ft., May 1938, Cheesman).

Measured specimens. Large ♂ holotype and large ♀ and small ♀ paratypes from Dobodura.

Notes. Although this is in some ways an excessively variable species, the characters used to define it in the key (above) appear to hold without exception.

IRIDAGONUM QUADRIPUNCTELLUM n. sp.

Description. With characters of genus as described above, except outer elytral intervals not or only slightly impressed. Form of average *Agonum s. s. Head* .68 & .68 width prothorax; eyes normally formed, moderately large and prominent; both pairs of supraocular setae present, posterior ones about between posterior edges of eyes. *Prothorax* moderately narrowed in front and behind; width/length 1.32 & 1.32; base/apex 1.24 & 1.22; anterior angles only normally prominent; sides broadly arcuate, straighter (converging) and usually slightly sinuate toward base; basal angles obtuse, almost rounded-out; lateral margins moderate, broader toward base, only slightly reflexed; basal foveae broad, shallow, not sharply defined, punctate, the punctation extending (more sparsely) onto sides of pronotum before foveae; disc about as in *quadripunctum*. *Elytra* of average width and convexity, not impressed on disc; basal margin distinctly but obtusely angulate at humeri; apical-sutural denticles small but distinct; striae moderately impressed, faintly or not punctulate; 8th interval usually vaguely impressed in part only, 7th usually not impressed; 3rd interval 2-punctate (anterior puncture missing). *Measurements:* length 8.2–9.0; width 3.0–3.5 mm.

Types. Holotype ♂ (M.C.Z. No. 28,635) and 7 paratypes all from Aitape, **N-E. N. G.**, Aug. 1944 (Darlington).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. Sufficiently defined in the key, above.

IRIDAGONUM SEXPUNCTUM n. sp.

Description. With characters of genus as described above. Form of *Agonum s. s.* (more slender than *quadripunctum*), but somewhat variable. *Head* .61, .62, & .65 width prothorax; eyes normally formed, only moderately large and prominent; both pairs supraocular setae present, posterior ones about between posterior edges of eyes. *Prothorax* longer than in *quadripunctum*, rather strongly narrowed in front, less so behind; width/length 1.27, 1.30, 1.18; base/apex 1.40, 1.41, & 1.30; anterior angles more prominent than in *quadripunctum* (so that prothorax seems longer than figures suggest), acute but with apices narrowly rounded; sides broadly (variably) arcuate for much of length, more or less straight and slightly converging and often slightly and broadly sinuate before base; basal angles somewhat obtuse but well defined, only a little blunted; lateral margins moderate, not sharply defined, wider and a little more reflexed toward base; basal foveae shallow, more or less lightly punctate; disc as in *quadripunctum*. *Elytra* relatively long (in genus), with sides nearly parallel at middle; disc usually very slightly impressed about ⅓ from base; basal margin strongly, about rectangularly angulate at humeri; denticles at sutural angles smaller than in *quadripunctum*; striae lightly impressed, not or only faintly punctulate; outer elytral intervals longitudinally impressed about as in *quadripunctum*; 3rd interval 3-punctate, the punctures about normally placed. *Measurements:* length 10.2–12.2; width 3.6–4.4 mm.

Types. Holotype ♂ (British Mus.) and 10 paratypes (some in M.C.Z. No. 28,636) from Mt. Cyclops, Cyclops Mts., **Neth. N. G.**, 3,500 ft., Mar. 1936 (Cheesman). Also the following additional paratypes from **Neth. N. G.**: 6, Mt. Lina, Cyclops Mts., 3,500–4,500 ft., Mar. 1936 (Cheesman); 1, simply Cyclops Mts., 3,400–4,500 ft., Mar. 1936 (Cheesman); 1, Araucaria Camp, Snow Mts., 800 m. (about 2,600 ft.), Mar. 1939 (Toxopeus); 6, Rattan Camp, Snow Mts., 1,150 & 1,200 m. (about 3,750 & 3,900 ft.), Feb.–Mar. 1939 (Toxopeus); 1, Sigi Camp, Snow Mts., 1,500 m. (about 4,875 ft.), Feb. 24, 1939 (Toxopeus); 1, Mist Camp, Snow Mts., 1,800 m. (about 5,850 ft.), Jan. 1939 (Toxopeus).

Other material. One ♀, Chimbu Valley, Bismarck Range, **N-E. N. G.**, 5,000–7,500 ft., Oct. 1944 (Darlington). This probably represents at least a distinct subspecies, but I do not care to describe it without more material because of the great individual variation of some species of this genus.

Measured specimens. A large ♂, large ♀, and smaller and narrower ♂, all from the Cyclops Mts.

Notes. This variable species seems to be constant in at least the characters given in the key to species, above.

IRIDAGONUM SUBFUSUM n. sp.

Description. With characters of genus as described above. Broadly subfusiform, more attenuate in front than behind. *Head* .63 width prothorax; eyes a little smaller but more abruptly prominent than usual; anterior supraocular setae absent, posterior ones somewhat behind line of posterior edges of eyes. *Prothorax* strongly narrowed in front, only slightly so behind; width/length 1.21; base/apex 1.47; anterior angles prominent and acute except slightly rounded at tips; sides slightly arcuate at middle, nearly straight anteriorly and posteriorly, slightly sinuate near base; basal angles somewhat obtuse but well defined, only slightly blunted; lateral margins as usual in genus; basal foveae slightly deeper than usual, only vaguely punctate; disc as in other species; anterior marginal line almost entire, posterior one absent. *Elytra* rather wide, more convex than usual, scarcely impressed before middle; basal margin about rectangular at humeri; sutural angles with rudimentary denticles; striae deeply impressed, not punctate; outer intervals more lightly and briefly longitudinally impressed than in *quadripunctum* and *sexpunctum*; 3rd interval 3-punctate. *Male copulatory organs:* Fig. 45. *Measurements:* length 12.4; width about 5.0 mm.

Type. Holotype ♂ (Leiden Mus.) from Ibele (Iebele) Camp, Snow Mts., **Neth. N. G.**, 2,250 m. (about 7,325 ft.), Nov.–Dec. 1938 (Toxopeus); unique.

Measured specimen. The type.

Notes. In form, modification of eyes, and loss of anterior supraocular setae this interesting species parallels certain *Fortagonum* (*bufo* etc.) (see below) which also occur at high altitudes on the Snow Mts., but there is probably no direct relationship.

ALTAGONUM new genus

Diagnosis. Small or medium-sized (5.3–13.7 mm.); very variable in form, often *Agonum*- or *Calathus*-like, sometimes *Europhilus*- or *Sphodrus*-like or fusiform; variable also in color, usually black or brown, rarely with elytra green (*cheesmani*) or purplish (*regiscapha*), elytra sometimes broadly margined with pale but never mottled or blotched, sometimes (but not usually) more or less iridescent; wing-and-seta formula +w, ++, − (+), (+) (+) (+); see also key to genera.

Description. Size, form, and color as described above; upper surface usually impunctate (sometimes punctate in basal foveae of pronotum); microsculpture variable. *Head* more variable in form than in *Notagonum*, often a little more elongate; eyes variable, usually at least moderately large and prominent, but sometimes reduced in size or prominence; both pairs supraocular setae always present, posterior pair usually about between posterior edges of eyes, but relatively farther back when eyes reduced; head otherwise about as in *Notagonum*. *Prothorax* variable in form; anterior-lateral setae always absent, posterior-lateral ones usually present but absent in *nudicolle* and *fatuum*; prothorax otherwise essentially as in *Notagonum*; further details as described for species below. *Elytra* variable in form; basal margin entire, rounded or variably angulate at humeri; apices variable; striae normal; intervals usually not much modified toward apex, but outer ones sometimes (*pallinox*, *sphodrum*, etc.) longitudinally sulcate at least apically; 3rd interval usually normally 3-punctate, sometimes 2-punctate with anterior puncture absent, rarely impunctate (*fatuum* only). *Inner wings* always fully developed. *Lower surface* usually impunctate or nearly so; abdomen usually not pubescent, but with moderate or extensive pubescence in a few cases (*pubinox, pallinox, noctellum,* & *planinox; sphodrum* & *postsulcatum*); prosternal process simple. *Legs* including tarsi as in *Notagonum*, but 4th hind-tarsal segment usually simply emarginate, and if lobed (*caducum, cheesmani, scapha, nudicolle*) lobes very short, but with outer lobe still usually slightly longer than inner one; 5th hind-tarsal segment without obvious accessory setae but always or almost always with minute, very inconspicuous, perhaps vestigial ones (as in at least some *Notagonum*); claws simple. *Secondary sexual characters* normal. *Male copulatory organs* as figured (Figs. 46–51).

Genotype. Altagonum caducum n. sp. (below).

Generic distribution. Numerous in New Guinea, chiefly in the mountains; further range not determined.

Notes. Like *Notagonum*, this is a genus of convenience, distinguished from *Notagonum* by only one constant detail, absence of the anterior-lateral pronotal setae. This character is not of itself of generic value, and the group which it defines is, as I have indicated, not entirely a natural one. However its recognition is useful. The group is a transitional one which bridges the gap between the more generalized lowland Agonini of New Guinea, especially *Notagonum,* and several well-marked groups of mountain species, here called genera, characterized by further loss of setae, loss of wings, and in other ways. *Altagonum* is intermediate in altitudinal distribution as well as in structure. The majority of *Notagonum* occur at low altitudes, although there are also some which occur high in the mountains. But of *Altagonum* only one species (*vallicola*) seems to occur regularly at lowest altitudes and only one other (*grossulum*) was found even rarely at Dobodura. Most species of the genus are chiefly or entirely confined to middle and high altitudes. Their structure is correlated with their distribution. In several ways (loss of setae, modification of eyes in some cases, partial or complete loss of well-developed lobes of the 4th hind-tarsal segments) they show the beginnings of the effect of the mountain environment on what were obviously originally normal Agonini. These same changes, and eventually also loss of wings and other changes, have occurred among mountain Carabidae, especially Agonini, in many other parts of the world, as I have mentioned in the introduction to the present paper. The few species of *Altagonum* that I have myself collected in sufficient numbers to be sure of their habitats (*vallicola, sphodrum, nudicolle*) all occur on the ground in heavy forest, and are not associated with running or standing water. This is probably the habitat of most species of the genus, although some may depart from it.

One species evidently referable to this genus has been previously described, but I do not recognize it in the material before me. It is

Altagonum papuense (Sl.)

Platynus papuensis Sloane 1890, Records Australian Mus. **1**, p. 103.
Colpodes papuensis Sloane 1907, Deutsche Ent. Zeits., p. 179.

Type. From St. Joseph's River District, on the south coast of Papua about opposite Yule Is.; probably in the Australian Mus. at Sydney, Australia.

Occurrence in New Guinea. Known only from the type.

Notes. This is a rather large (9 by 3½ mm.), black, *Agonum*-like form, with 3rd elytral interval 2-punctate (anterior puncture absent). It may be a form of the species here called *vallicola,* but if so it is probably not identical with any of the subspecies here described: it is larger than typical *vallicola,* probably broader than subspecies *huonis,* and apparently without the iridescence of subspecies *subvividum.* Its locality (the south coast of New Guinea) is consistent with its being a fourth subspecies of the group. But Sloane, in his careful description of *papuense,* mentions no angulations of the elytral apices, which suggests that he had before him a distinct species which I have not seen. There is no use in guessing further about this now. For the present it seems better not to assign the name at all than to risk assigning it wrongly. The species is not included in the following key.

Key to the Species of Altagonum of New Guinea

1. Posterior-lateral pronotal setae present 2
— Posterior-lateral pronotal setae absent 23
2. Plain black or brown, *Agonum*-like forms, not fusiform; prothorax normally formed, at least moderately narrowed behind, with posterior angles obtuse or rounded 3
— Not as above in one or more details 14
3. Third elytral interval 2-punctate (anterior puncture absent) 4
— Third elytral interval 3-punctate 6
4. Black, lateral margins of prothorax and elytra not much paler, legs dark; elytral apices strongly angulate . . . . *vallicola*
    (4a) Smaller (6.8–7.9 mm.); not distinctly iridescent (p. 190) . . . . (*vallicola s. s.*)
    (4b) Larger (8.3–9.0 mm.); more slender; faintly iridescent (p. 190) . . . . . (subsp. *huonis*)
    (4c) Still larger (9.1–9.7 mm.); broad as typical form; more strongly iridescent (p. 191) . . . . (subsp. *subvividum*)
— Brownish-black, lateral margins of prothorax and elytra yellowish-translucent, legs yellowish-brown; elytral apices not angulate 5
5. Broader, prothoracic width/length 1.47–1.54; length 5.3–6.7 mm. . . . . *grossulum*
    (5a) Reticulate microsculpture (at 54×) faint or almost absent on disc of pronotum, distinct and moderately transverse on elytra; latter not iridescent (p. 191) . . . . (*grossulum* s. s.)
    (5b) Microsculpture distinct on pronotum, indistinguishable (at 54×) on elytra; latter not distinctly iridescent (p. 193) . . . . . (subsp. *reticolle*)
    (5c) Microsculpture of pronotum light and variable, of elytra indistinct (at 54×); elytra and sometimes also pronotum iridescent (p. 193) (subsp. *intensum*)
— Narrower, prothoracic width/length 1.31–1.40; length 6.4–7.5 mm. (p. 194) *grossuloides*
6. Basal margin of elytra obtusely angulate at humeri; length 6.5–10.6 mm. (if less than 9.0 mm., abdomen pubescent) 7
— Basal margin of elytra rectangular or nearly so at humeri (points of angles sometimes slightly blunted); length 6.6–7.9 mm. (abdomen not pubescent) 13
7. Abdomen not pubescent; length 9.0–10.6 mm. 8
— Abdomen pubescent at least near middle basally; length 6.5–9.0 mm. . . . 10
8. Length 9.0–9.5 mm. (p. 194) . . . . *nox*
— Larger, relatively a little broader; (see also descriptions) 9
9. Lateral margins of prothorax not obviously pale (p. 195) . . . . *magnox*

— Lateral margins of prothorax yellowish-translucent; (see also description) (p. 196)........ *japenox*

10. Length 8.1–9.0 mm. (p. 196)........ *pubinox*

— Size smaller; (see also descriptions)........ 11

11. Outer elytral intervals longitudinally impressed at least toward apex (p. 200)........ *pallinox*

— Outer elytral intervals not longitudinally impressed........ 12

12. Basal foveae of pronotum moderately impressed (p. 197)........ *noctellum*

— Basal foveae of pronotum scarcely impressed, flat (p. 198)........ *planinox*

13. Broad *Agonum*-like; prothoracic width/length 1.29–1.34 (p. 198)........ *dilutipes*

— More slender *Europhilus*-like; prothoracic width/length 1.15 & 1.18 (p. 199)........ *europhilum*

14. Elytra not broadly margined with pale........ 15

— Elytra broadly margined with pale........ 22

15. Apex of each elytron drawn out into a single, short, acute spine nearly in line of sutural interval, the spines slightly dehiscent; (see also description (p. 201)........ *tutum*

— Elytra with apices simple, or armed differently from above........ 16

16. Not strikingly fusiform; elytra not metallic........ 17

— Fusiform; elytra sometimes (not always) green or purplish........ 20

17. Outer elytral intervals not much modified toward apex (p. 202)........ *caducum*

— Elytral intervals 7, 8, & 9 longitudinally impressed at least toward apex. 18

18. Prothorax subquadrate, relatively narrow, width/length 1.18 & 1.20 in measured specimens; base/apex 1.28 & 1.20; (abdomen pubescent) (p. 204)........ *sphodrum*

— Prothorax wider, more narrowed in front, width/length 1.30–1.44, base/apex 1.40–1.47........ 19

19. Apices of elytra unarmed or with at most small sutural denticles; abdomen pubescent at least near middle basally (p. 205)........ *postsulcatum*

— Apex of each elytron with 2 prominent denticles; abdomen not pubescent (p. 206)........ *misim*

20. Elytra green, (spined); eyes very prominent, head .80 width prothorax (p. 207)........ *cheesmani*

— Elytra black or purplish, (spined or angulate at apices); eyes less prominent, head .65 or less width prothorax........ 21

21. Elytra black; posterior-lateral pronotal setae on flat surface of margins well in from edges (p. 208)........ *scapha*

— Elytra purplish; posterior-lateral pronotal setae on edges of margins (p. 209)........ *regiscapha*

22. Broader; prothoracic width/length 1.48 & 1.44 in measured specimens; dark discal color of elytra not extending in a narrow sutural stripe toward apex (p. 210)........ *latilimbus*

— More slender; prothoracic width/length 1.32 & 1.34; dark discal color of elytra extending along sutural intervals toward (not to) apex (p. 211) *paralimbus*

23. Form rather broad *Calathus*-like; 3rd elytral interval 3-punctate (p. 211) *nudicolle*

— Form slender; 3rd elytral interval impunctate (p. 212)........ *fatuum*

ALTAGONUM VALLICOLA n. sp.

Description. With characters of genus as described above. Form of broad *Agonum s. s.*; black, appendages brownish-black, lateral margins of prothorax and elytra only slightly translucent; upper surface impunctate except vaguely punctate in basal foveae and on lateral margins of pronotum, moderately shining, not distinctly iridescent; microsculpture lightly impressed, normal (isodiametric on head, transverse on pronotum, more transverse on elytra). *Head* .61 & .66 width prothorax; eyes large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* large and wide; width/length 1.55 & 1.44; base/apex 1.43 & 1.42; sides strongly arcuate for most of length, nearly straight and converging and sometimes slightly sinuate before basal angles; latter obtuse, moderately rounded; lateral margins rather wide, wider and more reflexed toward base; basal foveae normal, vaguely punctate; disc normal; anterior and posterior marginal lines entire or nearly so. *Elytra* moderately wide, normal in outline and convexity, not or faintly impressed before middle; basal margin usually vaguely subangulate at humeri; lateral margins rather wide; subapical sinuations moderate; apices prominently angulate about opposite 3rd intervals, these angulations more prominent than sutural ones; apices then obliquely subtruncate to finely denticulate sutural angles; striae variably, usually rather lightly impressed, not or faintly punctulate; intervals nearly flat or slightly convex, 8th and 9th not much modified toward apex; 3rd interval 2-punctate (anterior puncture absent). *Lower surface* virtually impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment emarginate, not lobed. *Male copulatory organs:* Fig. 46. *Measurements:* length 6.8–7.9; width 2.8–3.1 mm.

Types. Holotype ♂ (M.C.Z. No. 28,637) and 25 paratypes all from Dobodura, **Papua**, Mar.–July 1944 (Darlington); taken among dead leaves on the ground in heavy rainforest in company with superficially similar *Notagonum spinulum.*

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. Sufficiently discussed and defined under the genus and in the key to species, above. Perhaps it should be added that small specimens of this species are extremely similar to *Notagonum subspinulum* except that they lack the anterior-lateral pronotal setae and have the elytral apices armed with only acute teeth rather than short spines.

ALTAGONUM VALLICOLA HUONIS n. subsp.

Description. Similar to typical *vallicola* in all details except a little larger, obviously more elongate, and with faint iridescence on elytra in strong light. *Head* .67 & .69 width prothorax. *Prothorax:* width/length 1.39 & 1.39; base/apex 1.46 & 1.47; sides less strongly rounded than in typical *vallicola,* and basal angles correspondingly more distinct, though still obtusely rounded. *Elytra* more slender and elongate, with basal margin a little more distinctly angulate at humeri. *Measurements:* length 8.3–9.0; width 3.1–3.4 mm.

Types. Holotype ♂ (M.C.Z. No. 28,638) from (hills north of) Nadzab, **N-E. N. G.**, July 1944 (Darlington); and 1 ♂ paratype from Sattelberg, **N-E. N. G.** (British Mus., ex Coll. G. Hauser).

Measured specimens. The types.

Notes. Sufficiently compared with typical *vallicola* above.

ALTAGONUM VALLICOLA SUBVIVIDUM n. subsp.

Description. Similar to typical *vallicola* in all details except larger, with elytra a little more distinctly (but variably) impressed before middle, a little more deeply striate, and more or less strongly iridescent. *Head* .63 & .64 width prothorax. *Prothorax:* width/length 1.41 & 1.42; base/apex 1.46 & 1.55; sides rather strongly rounded. *Elytra* less elongate than in *huonis,* a little more deeply striate than usual in typical *vallicola* or *huonis,* and rather strongly iridescent, with elytral microsculpture not distinguishable at 54× and probably too fine and transverse to see. *Measurements:* length (types) 9.1–9.7; width (types) 3.4–3.7 mm.

Types. Holotype ♂ (British Mus.) and 4 paratypes (2 in M.C.Z. No. 28,639) all from Mt. Baduri, Japen Is., **Neth. N. G.**, 1,000 ft., Aug. 1938 (Cheesman).

Other material. All from **Neth. N. G.**, as follows: 1, Hollandia, July–Sept. 1944 (Darlington); 4, Mt. Sabron, Cyclops Mts., 2,000 ft., June & July 1936 (Cheesman); 2, Rattan Camp, Snow Mts., 1,150 & 1,200 m. (about 3,750 & 3,900 ft.), Feb.–Mar. 1939 (Toxopeus); and 1, "New Guinea" (H. E. Andrewes Coll., British Mus., labeled "*Colpodes sp.*"). These specimens, though referable to this subspecies, are a little smaller and/or less strongly iridescent than the types.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. Sufficiently compared with typical *vallicola* and subspecies *huonis* above.

ALTAGONUM GROSSULUM n. sp.

Description. With characters of genus as described above. Form of small but very broad *Agonum s. s.*; brownish-black, appendages yellowish-brown, lateral margins of prothorax and elytra yellowish-translucent; upper surface virtually impunctate, moderately shining, not iridescent; microsculpture distinct and isodiametric on head, almost absent or faint on disc of pronotum, distinct and moderately transverse on elytra. *Head* .61 & .63 width prothorax; eyes large and prominent, with posterior supraocular setae slightly before line of their posterior edges. *Prothorax* relatively large and wide; width/length 1.54 & 1.50; base/apex 1.31 & 1.43; sides nearly evenly, rather strongly arcuate for entire or nearly entire length; basal angles obtuse, moderately rounded; lateral margins rather wide, but not much more reflexed toward base; basal foveae rather broad and shallow, vaguely or not distinctly punctate; disc normal, with anterior marginal line entire, posterior one more or less entire but sometimes vague at middle. *Elytra* broad, otherwise of normal outline and convexity, distinctly impressed before middle; basal margin obtusely angulate or blunted at humeri; lateral margins rather wide (in genus); subapical sinuations moderate or slight; apices nearly simple, somewhat irregularly rounded, with sutural angles not or sometimes vaguely denticulate; striae well impressed, impunctate; intervals more or less convex, 8th and 9th not much modified toward apex, 3rd 2-punctate (anterior puncture absent). *Lower surface* virtually impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment simply emarginate, not lobed. *Measurements:* length 5.4–6.5; width 2.3–2.8 mm.

Types. Holotype ♂ (M.C.Z. No. 28,640) and 2 ♂♂ paratypes from Dobodura, **Papua**, Mar.–July 1944 (Darlington); and additional paratypes as follows: **Papua:** 1, Kokoda, 1,200 ft., Aug. 1933 (Cheesman); 2, Mafulu, 4,000 ft., Dec. 1933 & Jan. 1934 (Cheesman). **N-E. N. G.:** 1, Nadzab ("E. fork Ngafir Cr. 1,000–3,000 ft. native trail"), July 13, 1944 (K. V. Krombein, U.S.N.M.).

Other material. Two additional subspecies described below; and 1 specimen from Mt. Nok, Waigeo Is., **Neth. N. G.**, 2,500 ft., May 1938 (Cheesman), which does not fit into any of the subspecies here recognized.

Measured specimens. The ♂ holotype and 1 ♂ paratype from Dobodura.

Notes. This species is distinguished from all related forms known to me by its small size and relatively broad but still *Agonum*-like form, plus details given in the key to species. The present, typical subspecies is distinguished from the others described below by having the disc of the pronotum more shining, without or with only faint traces of reticulate microsculpture, and the elytra with comparatively coarse and obvious microsculpture (most obvious in the Kokoda and Dobodura specimens, finer but still visible in the Mafulu and Nadzab ones) and no or only very slight iridescence. I do not know the ecological habitat of this species. Although it does occur, rarely, near sea level at Dobodura, it (as represented by the following subspecies) seems to be much commoner in foothills and lower mountains.

ALTAGONUM GROSSULUM RETICOLLE n. subsp.

Description. Size, form, and structural details almost as in typical *grossulum*, but microsculpture of upper surface different, as follows: on head, about same; on disc of pronotum, meshes distinct though somewhat variably so, moderately transverse (not faint or absent as in typical *grossulum*); on elytra, so fine as not to be visible at 54× (not distinct as in typical *grossulum*), but in spite of fineness of microsculpture of elytra, latter not or only faintly iridescent even in strong light. *Head* .65 & .63 width prothorax. *Prothorax:* width/length 1.51 & 1.51; base/apex 1.32 & 1.38. *Measurements:* length 5.7–6.7; width 2.4–2.8 mm.

Types. Holotype ♂ (British Mus.) and 4 paratypes (2 in M.C.Z. No. 28,641) from Sabron, Cyclops Mts., **Neth. N. G.**, 2,000 ft., June & July 1936 (Cheesman); 2 paratypes from Mt. Lina, Cyclops Mts., 3,500–4,500 ft., Mar. 1936 (Cheesman).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Sabron.

Notes. Sufficiently compared with typical *grossulum* above.

ALTAGONUM GROSSULUM INTENSUM n. subsp.

Description. Size, form, and structural details almost as in typical *grossulum* and subspecies *reticolle*, but pronotum sometimes and elytra always rather strongly iridescent; microsculpture of head as in preceding forms, of prothorax light and variable, of elytra not distinctly visible at 54× but probably very fine and transverse. *Head* .66 & .62 width prothorax. *Prothorax:* width/length 1.48 & 1.51; base/apex 1.41 & 1.47. *Measurements:* length 5.3–6.7; width 2.3–2.9 mm.

Types. Holotype ♂ (British Mus.) and 18 paratypes (some in M.C.Z. No. 28,642) from Mt. Baduri, Japen Is., **Neth. N. G.**, 1,000 ft., Aug. 1938 (Cheesman).

Other material. Nine, Rattan Camp, Snow Mts., **Neth. N. G.**, 1,150 m. (about 3,750 ft.), Feb.–Mar. 1939 (Toxopeus); and 1, Lower Mist Camp, Snow Mts., 1,700 m. (about 5,525 ft.), Jan. 17, 1939 (Toxopeus). These specimens average a little larger and somewhat less strongly iridescent than the types.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. Sufficiently compared with other subspecies above and in the key to species of *Altagonum*.

ALTAGONUM GROSSULOIDES n. sp.

Description. Extremely similar to *A. grossulum*, and answering to the description of the latter (see above) in every detail not mentioned below, but more slender, with prothorax especially narrower. *Head* .67 & .64 width prothorax. *Prothorax:* width/length 1.31 & 1.39 (5 other specimens 1.34 to 1.40); base/apex 1.50 & 1.48; sides much more weakly arcuate than in *grossulum* and a little more narrowly margined. *Elytra* as in *grossulum*. *Measurements:* 6.4–7.5; width 2.6–3.0 mm.

Types. Holotype ♂ (Leiden Mus.) and 8 paratypes (some in M.C.Z. No. 28,643) from Mist Camp, Snow Mts., **Neth. N. G.**, 1,800 m. (about 5,850 ft.), Jan. (1 paratype Feb. 3) 1939 (Toxopeus). Also the following paratypes, all from **Neth. N. G.:** 3, Rattan Camp, Snow Mts., 1,150 m. (about 3,750 ft.), Feb.–Mar. 1939 (Toxopeus); 3, Top Camp, Snow Mts., 2,100 m. (about 6,825 ft.), Jan. 27, 1939 (Toxopeus); 4, Mt. Lina, Cyclops Mts., 3,500–4,500 ft. (2 specifically from 4,500), Mar. 1936 (Cheesman); 1, Cyclops Mts. without more exact locality, 3,400–4,500 ft., Mar. 1936 (Cheesman); and 2, Mt. Baduri, Japen Is., 1,000 ft., Aug. 1938 (Cheesman).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Mist Camp.

Notes. If this were geographically separated from *grossulum*, I might consider it merely a subspecies of the latter, but since the two occur in the same areas they are presumably distinct species. There is no overlapping of prothoracic ratios: width/length of prothorax in 9 measured specimens of *grossulum* (including all subspecies) is 1.47 to 1.54; in 7 of *grossuloides*, 1.31 to 1.40. *Grossuloides* tends to be larger than *grossulum* and to occur at higher altitudes, but these are not absolute differences.

ALTAGONUM NOX n. sp.

Description. With characters of genus as described above. Form of rather large *Agonum s. s.*; black, appendages only slightly paler, lateral margins of prothorax and elytra scarcely translucent; upper surface impunctate except sometimes more or less vaguely punctate in and near pronotal foveae, moderately shining, elytra slightly or faintly iridescent; microsculpture fine but apparently normal in form. *Head* .64 & .64 width prothorax; eyes moderately large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* rather large and wide; width/length 1.45 & 1.43; base/apex 1.47 & 1.40; sides moderately arcuate for much of length, nearly straight and moderately converging and sometimes slightly sinuate toward base; basal angles obtuse but well defined, only slightly blunted;

lateral margins rather wide especially toward base, moderately reflexed; basal foveae rather deep, not or vaguely punctate; disc normal; anterior and posterior marginal lines entire, the posterior one more lightly impressed. *Elytra* of normal outline and convexity, not or vaguely impressed before middle; basal margin obtusely angulate at humeri; lateral margins average; subapical sinuations rather weak; apices rather narrowly rounded to slightly or not distinctly denticulate sutural angles; striae moderately impressed, not punctate; intervals somewhat convex, 8th and 9th not much modified toward apex, 3rd 3-punctate with punctures normally placed. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment rather deeply emarginate but without produced lobes. *Measurements:* length 9.0–9.5; width 3.3–3.5 mm.

Types. Holotype ♂ (Leiden Mus.) and 5 paratypes (2 in M.C.Z. No. 28,644) all from Mist Camp, Snow Mts., **Neth. N. G.**, 1,800 m. (about 5,850 ft.), Jan. (type Jan. 18, 1 paratype Jan. 4) and Feb. 10, 1939 (Toxopeus).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This species, which is of course differentiated from others in the key to species, above, will be taken as the standard of comparison for several more or less similar, following forms.

ALTAGONUM MAGNOX n. sp.

Description. Very close to *nox* and answering to the same description (see above) in all details except those noted below. Larger and a little broader; basal foveae and margins of pronotum before them a little more distinctly punctate; elytra a little more iridescent. *Head* .64 & .60 width prothorax. *Prothorax* a little more narrowed in front and less narrowed behind, with sides less converging toward base; width/length 1.38 & 1.45; base/apex 1.56 & 1.59. Other characters as in *nox*. *Male copulatory organs:* Fig. 47. *Measurements:* length 10.6; width 4.2 mm. (both specimens).

Types. Holotype ♂ (Leiden Mus.) from Rattan Camp, Snow Mts., **Neth. N. G.**, 1,200 m. (about 3,900 ft.), Feb.–Mar. 1939 (Toxopeus); and 1 ♀ paratype (M.C.Z. No. 28,645) from Mist Camp, Snow Mts., 1,800 m. (about 5,850 ft.), Feb. 3, 1939 (Toxopeus).

Measured specimens. The types.

Notes. The only characters distinguishing this species from *nox* to which I can give exact expression are the larger size and relatively greater ratio of base/apex of prothorax. The difference in form of prothorax is obvious to the eye.

ALTAGONUM JAPENOX n. sp.

Description. Again very close to *nox*, and answering to the description of the latter (see above) in all details except those noted below. Larger and a little wider than *nox*; legs browner, lateral margins of prothorax yellowish-translucent; elytra more obviously iridescent. *Head* .58 & .58 width prothorax. *Prothorax* relatively a little wider; width/length 1.51 & 1.51; base/apex 1.50 & 1.50. *Measurements:* length 9.9–10.2; width about 3.9 mm.

Types. Holotype ♀ (British Mus.) and 1 ♀ paratype (M.C.Z. No. 28,646) both from Mt. Baduri, Japen Is., **Neth. N. G.**, 1,000 ft., Aug. 1938 (Cheesman).

Measured specimens. The types.

Notes. This species is perhaps even closer to *magnox* (above) than to *nox*, the base-species with which I have compared it. The principal characters distinguishing *japenox* from *magnox* are the obviously pale-translucent prothoracic margins and the relatively slightly narrower head and wider prothorax as shown by the ratios given. It remains to be seen to what extent these differences will hold in series. *Japenox* may prove to be a subspecies of *magnox*, but I am not sufficiently sure of relationships in this group of *Altagonum* to make it a subspecies now.

ALTAGONUM PUBINOX n. sp.

Description. Again close to *nox*, and answering to the description of the latter (see above) in all details except those noted below. A little smaller and much narrower than *nox*, with elytra obviously impressed before middle and at most only faintly iridescent. *Head* .70 & .70 width prothorax. *Prothorax* much narrower than in *nox;* width/length 1.27 & 1.27; base/apex 1.38 & 1.42; sides rather weakly arcuate for most or all of length, moderately converging and sometimes nearly straight or even faintly sinuate posteriorly; basal angles more obtuse and more blunted than in *nox* primarily because sides of base (in *pubinox*) more rounded-oblique; lateral margins narrower than in *nox*. *Lower surface* as in *nox* except abdomen with a little pubescence near middle of at least basal segments. *Measurements:* length 8.1–9.0; width 3.0–3.4 mm.

Types. Holotype ♂ (Leiden Mus.) and 7 paratypes (some in M.C.Z. No. 28,647) from Sigi Camp, Snow Mts., **Neth. N. G.**, 1,500 m. (about 4,875 ft.), Feb. (type & 3 paratypes specifically Feb. 19, 2 paratypes Feb. 25) 1939 (Toxopeus); and the following additional paratypes from the Snow Mts.: 1, Lower Mist Camp, 1,700 m. (about 5,525 ft.), Jan. 17, 1939 (Toxopeus); 1, Mist Camp, 1,800 m. (about 5,850 ft.), Jan. 1939 (Toxopeus).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Sigi Camp.

Notes. Although this species differs from *nox* (and from *magnox* and *japenox*) by presence of a little pubescence near middle of at least the basal ventral abdominal segments, other characters are so similar that I think the relationship to *nox* is probably close.

ALTAGONUM NOCTELLUM n. sp.

Description. Again close to *nox*, and answering to the description of the latter (see above) in all details except those noted below. Much smaller, somewhat narrower, and a little more brownish (less deep black) than *nox*; elytra slightly, sometimes indistinctly impressed before middle, at most faintly iridescent. *Head* .77 & .76 width prothorax. *Prothorax* relatively much narrower than in *nox*; width/length 1.24 & 1.29; base/apex 1.34 & 1.35; sides weakly arcuate anteriorly, straight or slightly sinuate and only moderately converging toward base; basal angles much more obtuse or rounded than in *nox*, chiefly because sides of base rather strongly oblique; lateral margins slightly narrower and less reflexed than in *nox*, and basal foveae shallower, but still moderately impressed. *Lower surface* as in *nox* except abdomen with a little pubescence near middle of at least basal segments. *Measurements:* length 6.8–7.9; width 2.5–2.9 mm.

Types. Holotype ♂ (British Mus.) and 2 paratypes (♂ in M.C.Z. No. 28,648) from Cyclops Mts., **Neth. N. G.**, 3,400–4,500 ft., Mar. 1936 (Cheesman); 3 paratypes from Mt. Lina, Cyclops Mts., 3,500–4,500 ft., Mar. 1936 (Cheesman); and 2 paratypes from Rattan Camp, Snow Mts., 1,200 m. (about 3,900 ft.), Feb.–Mar. 1939 (Toxopeus).

Other material from **Neth. N. G.** as follows: 1, Sabron, Cyclops Mts., 2,000 ft., May 1936 (eyes abnormally prominent) (Cheesman); 1, Camp Nok, Waigeo Is., 2,500 ft., Apr. 1938 (Cheesman).

Measured specimens. The ♂ holotype and 1 ♀ paratype from the Cyclops Mts.

Notes. Although I have compared this with what I have taken as the base-species of this group (*nox*), *noctellum* is actually closer to *pubinox*, which it resembles in ventral pubescence. It is in fact very close to *pubinox*, differing most obviously in smaller size, with head relatively slightly wider, pronotum a little less convex, and elytra less obviously impressed before the middle. It evidently occurs at slightly lower altitudes than *pubinox*. The two Snow Mts. specimens of *noctellum* are not intermediates but show all the characters of the species, including small size (both specimens under 7 mm.).

ALTAGONUM PLANINOX n. sp.

Description. A member of the *nox* group but with form more of *Europhilus* than of *Agonum s. s.* Answering technical description of *nox* (see above) in all details except those noted below. Much smaller, more slender, with flatter pronotum than *nox*; more brownish-black, appendages yellowish-brown, lateral margins of prothorax narrowly but distinctly yellowish-translucent; elytra slightly impressed before middle, at most faintly iridescent. *Head* .80 & .78 width prothorax; eyes a little more prominent than usual in group. *Prothorax* relatively small, subquadrate; width/length 1.36 & 1.38; base/apex 1.37 & 1.39; sides weakly arcuate, appearing subparallel, rather weakly converging and slightly or not sinuate basally; basal angles obtuse, blunted or rather narrowly rounded; lateral margins narrow, very little reflexed; basal foveae scarcely impressed, flat; disc flatter than in *nox*. *Elytra* with basal margin rounded or vaguely angulate at humeri; lateral margins narrow; outer intervals as in *nox*, not much modified toward apex. *Lower surface:* abdomen with some pubescence near middle of all segments. *Measurements:* length 6.5–7.5; width 2.6–2.9 mm.

Types. Holotype ♂ (British Mus.) and 5 paratypes (some in M.C.Z. No. 28,649) from Mt. Lina, Cyclops Mts., **Neth. N. G.**, 3,500–4,500 ft., Mar. 1936 (Cheesman); 2 paratypes, Cyclops Mts. without further locality, 3,400–4,500 ft., Mar. 1936 (Cheesman); and 1 paratype, Rattan Camp, Snow Mts., 1,150 m. (about 3,750 ft.), Feb.–Mar. 1939 (Toxopeus).

Other material. One specimen, Mafulu, **Papua**, 4,000 ft., Jan. 1934 (Cheesman).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Mt. Lina.

Notes. Set beside *nox* this species seems very different indeed, but there is a practically complete transitional series beginning in fact with *magnox* (and *japenox*) through *nox*, *pubinox*, and *noctellum* to the present species, and extending perhaps even to the following ones (*dilutipes* and *europhilum*), which may be transitional toward more fusiform species. The present species (*planinox*) differs from the preceding ones of the series in having paler legs and antennal bases, and a flatter pronotum with scarcely impressed basal foveae.

ALTAGONUM DILUTIPES n. sp.

Description. With characters of genus as described above. Broad *Agonum*- or *Stenolophus*-like; brownish-black, appendages yellowish-brown, lateral margins of prothorax and elytra yellowish-translucent;

upper surface impunctate except vaguely punctate in pronotal foveae, moderately shining, elytra iridescent; microsculpture about normal except indistinct (presumably very fine and transverse) on elytra. *Head* .71 & .65 width prothorax; eyes moderately large and prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* of moderate size; width/length 1.29 & 1.34; base/apex 1.24 & 1.28; sides moderately arcuate for most or all of length, sometimes nearly straight (and converging) toward base; basal angles broadly rounded, very obtuse or not at all defined; lateral margins moderate, wider basally, moderately reflexed; basal foveae average, vaguely punctate; disc normal; anterior and posterior marginal lines entire except posterior one sometimes vague near middle. *Elytra* rather broad, of normal outline and convexity, not or only faintly impressed before middle; basal margin strongly, almost rectangularly angulate at humeri (but points of angulations more or less blunted); lateral margins rather wide (in genus); subapical sinuations weak; apices rather narrowly rounded to subdenticulate sutural angles; striae moderately impressed, not punctate; intervals somewhat convex, 8th and 9th not much modified toward apex, 3rd normally 3-punctate. *Lower surface* impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment simply emarginate, not lobed. *Measurements:* length 6.6–7.8; width 2.5–3.0 mm.

Types. Holotype ♂ (British Mus.) and 3 paratypes (1 in M.C.Z. No. 28,650) from Mt. Lina, Cyclops Mts., **Neth. N. G.**, 3,500–4,500 ft., Mar. 1936 (Cheesman); 2 paratypes, Cyclops Mts. without further locality, 3,500 & 3,400–4,500 ft., Mar. 1936 (Cheesman); and 2 paratypes, Rattan Camp, Snow Mts., 1,150 & 1,200 m. (about 3,750 & 3,900 ft.), Feb.–Mar. 1939 (Toxopeus).

Measured specimens. The ♂ holotype, and 1 ♀ paratype from the Cyclops Mts.

Notes. This species is sufficiently distinguished from others in the key to species, above.

ALTAGONUM EUROPHILUM n. sp.

Description. With characters of genus as described above. Form of *Agonum* subgenus *Europhilus;* brownish-black, appendages somewhat paler, lateral margins of prothorax and elytra only slightly translucent; upper surface virtually impunctate, moderately shining, elytra not or faintly iridescent; microsculpture about normal. *Head* .67 & .70 width prothorax; eyes rather large but only a little prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* rather small, subquadrate, appearing almost as long as wide but width/length actually 1.15 & 1.18; base/apex about 1.41 & 1.32; sides slightly arcuate for most of length, nearly straight and slightly converging basally; posterior angles very obtuse, almost rounded out, partly because sides of base rounded-oblique; lateral margins narrow anteriorly, wider basally, slightly reflexed; posterior-lateral setae set a little in from edges of margins near posterior angles; basal foveae slightly impressed, not distinctly punctate; disc weakly convex, with middle line and transverse impressions only slightly impressed; anterior and posterior marginal lines nearly entire, but light and more or less interrupted at middle. *Elytra* long-oval, normally convex, only faintly impressed before middle; basal margin almost rectangular at humeri; lateral margins rather narrow; subapical sinuations almost obliterated, sides of elytra curving in almost evenly to subdenticulate sutural angles; striae moderately impressed, impunctate; intervals moderately convex, 8th and 9th not much modified toward apex, 3rd normally 3-punctate. *Lower surface* impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment simply emarginate. *Measurements:* length 7.8–7.9; width 2.8–2.9 mm.

Types. Holotype ♂ (Leiden Mus.) from Mist Camp, Snow Mts., **Neth. N. G.**, 1,800 m. (about 5,850 ft.), Jan. 1939 (Toxopeus); and 1 ♂ paratype (M.C.Z. No. 28,651) from Top Camp, Snow Mts., 2,100 m. (about 6,825 ft.), Jan. 26, 1939 (Toxopeus).

Measured specimens. The types.

Notes. This species may be related to both *dilutipes* and *planinox* (above), and through them to the *nox* group of *Altagonum,* but it differs in so many ways that I have given it a full description. The following is a list of the more important differences between the present species and *planinox:* head relatively narrower, with much less prominent eyes; prothorax longer, with posterior-lateral setae set in from edges of margins, and with less impressed anterior and posterior marginal lines; elytra more oval, with humeral margins much more strongly angulate, and with subapical sinuations almost obliterated; abdomen not pubescent. In the face of this list of differences it is obviously unwise to assume a real relationship between this species and *planinox*. The relationship with *dilutipes* is more probable. The present species has the form of a slender *Dicranoncus,* but the tarsal claws are not toothed.

ALTAGONUM PALLINOX n. sp.

Description. With characters of genus as described above. Form of a large, rather slender, somewhat depressed *Bembidion* or *Europhilus*; brown, head slightly darker, abdomen with irregular pale areas, appendages yellowish, lateral marginal gutters of prothorax and elytra narrowly yellowish; surface only moderately shining, not iridescent; microsculpture normal. *Head* .86 & .85 width prothorax; eyes large, prominent, with posterior supraocular setae about between their posterior edges. *Prothorax* somewhat transversely subquadrate or subcordate; width/length 1.34 & 1.38; base/apex 1.27 & 1.24; sides less arcuate than usual, moderately sinuate about 1/6 of length before base; basal angles slightly obtuse but well defined; lateral margins rather narrow; basal foveae poorly defined, only slightly impressed, slightly roughened but not punctate; anterior marginal line faint or interrupted at middle, posterior one vague. *Elytra* rather narrow, subparallel, a little less convex than usual, with disc broadly, vaguely impressed about 2/5 from base; basal margin rounded or faintly angulate at humeri; subapical sinuations moderate; apices moderately rounded, distinctly but finely and bluntly subdenticulate at sutural angles; striae rather deep, not distinctly punctulate; intervals convex, 8th and 9th and usually 7th longitudinally impressed or sulcate toward apex, 3rd normally 3-punctate. *Lower surface* virtually impunctate; abdomen with a little pubescence near middle near base. *Legs:* 4th hind-tarsal segment simply emarginate. *Measurements:* length 6.8–7.6; width 2.4–2.8 mm.

Types. Holotype ♂ (British Mus.) and 4 paratypes (2 in M.C.Z. No. 28,688) from Cyclops Mts., **Neth. N. G.**, 3,400–4,500 ft., Mar. 1936 (Cheesman). Additional paratypes as follows: **Neth. N. G.:** 1, Mt. Lina, Cyclops Mts., 3,500–4,500 ft., Mar. 1936 (Cheesman); 1, Cyclops Mts. without more exact data (Cheesman). **Papua:** 1, Mondo, 5,000 ft., Jan.–Feb. 1934 (Cheesman).

Measured specimens. The ♂ holotype and 1 ♀ paratype from the Cyclops Mts.

Notes. This is a very distinct species, distinguishable by characters given in the key. I have associated it with the *nox* group, but I am not sure there is a close relationship. The species has a remarkable superficial similarity to the *Notagonum* of the *angustellum* group, but it differs from them not only in absence of the anterior-lateral pronotal setae but also in impression of the outer elytral intervals toward apex and in form (simply emarginate) of the 4th hind-tarsal segment.

ALTAGONUM TUTUM n. sp.

Description. With characters of genus as described above. Form nearly that of small, rather slender *Agonum s. s.*; piceous-black, legs brownish-piceous, antennae browner, lateral margins of prothorax vaguely translucent; upper surface nearly impunctate, moderately shining, not iridescent; microsculpture normal, light on head and pronotum. *Head* .82 width prothorax; eyes large, moderately prominent, with posterior supraocular setae about between their posterior edges; neck-constriction vague. *Prothorax* rather small, subquadrate, widest about middle, rather strongly narrowed in front; width/length 1.23; base/apex 1.44; anterior angles scarcely advanced; sides moderately arcuate for much of length, rather broadly sinuate before base; basal angles approximately right but narrowly rounded; lateral margins rather narrow, moderately reflexed posteriorly; posterior-lateral setae on edges of margins at basal angles; basal foveae normal, vaguely punctate; disc normal; anterior and posterior marginal lines entire. *Elytra* normal in outline, a little more convex than usual, not impressed on disc; basal margin only vaguely angulate at humeri; lateral margins rather narrow; subapical sinuations moderate, each leading onto a short apical spine almost at sutural angle; striae well impressed, impunctate; intervals moderately convex, 8th and 9th not much modified toward apex, 3rd normally 3-punctate. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment simply emarginate. *Measurements:* length 7.7; width 2.8 mm.

Type. Holotype ♀ (British Mus.) from Mt. Nok, Waigeo Is., **Neth. N. G.**, 2,500 ft., May 1938 (Cheesman); unique.

Measured specimen. The type.

Notes. This is an inconspicuous but safely characterized species, placed in the key to species (above) but not closely related to any other species known to me. It may have originated independently from *Notagonum* by development of sutural spines and loss of the anterior-lateral pronotal setae.

ALTAGONUM CADUCUM n. sp.

Description. With characters of genus as described above. Form nearly of elongate *Calathus* (Fig. 6); brown to brownish-black, appendages brown, lateral margins of prothorax broadly and plainly, of elytra not distinctly yellowish-translucent; upper surface impunctate, moderately shining, not iridescent; microsculpture light and isodiametric on head, very light (sometimes scarcely visible) and transverse on disc of pronotum, distinct and transverse on elytra. *Head* .76, .74, & .73 width prothorax; eyes large and moderately prominent, with posterior supraocular setae about between their posterior edges; neck-constriction distinct but not deep. *Prothorax* strongly narrowed in front, only slightly so behind; width/length 1.33, 1.30, & 1.32; base/apex 1.46, 1.53, & 1.53; sides rather weakly arcuate for much of length, broadly but slightly sinuate before rectangular, scarcely blunted posterior angles; lateral margins rather wide especially toward base, moderately reflexed; posterior-lateral setae on edges of margins almost at basal angles; basal foveae rather deep, not or at most vaguely punctate; disc normal; anterior and posterior marginal lines entire. *Elytra* rather ample, of average outline and convexity, distinctly impressed before middle; basal margin obtusely angulate or subangulate at humeri; lateral margins narrow; subapical sinuations moderate or rather weak; apices each rounded-prominent about opposite 3rd interval, minutely denticulate or subdenticulate at sutural angle; striae moderately impressed, impunctate; intervals slightly convex, 8th and 9th not much modified toward apex, 3rd 3-punctate, punctures normally placed except posterior one often not so far back as usual (exact position variable in both Mt. Misim and Snow Mts. series). *Lower surface* virtually impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment with a short outer and still shorter inner lobe. *Male copulatory organs:* Fig. 48. *Measurements:* length 9.4–11.0; width about 3.5–4.1 mm.

Types. Holotype ♂ (M.C.Z. No. 28,652) and 8 paratypes from Mt. Misim, Morobe Dist., **N-E. N. G.** (Stevens). Additional paratypes from **Neth. N. G.** as follows: 2, Cyclops Mts., 3,400–4,500 ft., Mar. 1936 (Cheesman); and from the Snow Mts.: 8, Sigi Camp, 1,500 m. (about 4,875 ft.), Feb. 1939; 1, Lower Mist Camp, 1,700 m. (about 5,525 ft.), Jan. 17, 1939; 30, 1,800 m. (about 5,850 ft.), Dec. 30, 1938 & Jan. 1939; 2, Top Camp, 2,100 m. (about 6,825 ft.), Jan. 25 & 26, 1939; 1, Ibele (Iebele) Camp, 2,250 m. (about 7,325 ft.), Nov. 1938 (all Snow Mts. specimens collected by Toxopeus).

Measured specimens. Holotype ♂, 1 ♀ paratype from Mt. Misim, & 1 ♂ paratype from Mist Camp, Snow Mts.

Notes. Although not a striking species, this is a very distinct one apparently not closely related to any other known to me. It may lead toward *sphodrum* etc. (below), but the outer elytral intervals are not impressed as they are in the *sphodrum* group; the abdomen is not pubescent as it is in *sphodrum* and its closest ally, *postsulcatum*; and the 4th hind-tarsal segment is different, briefly lobed externally in *caducum*, but simply emarginate in the *sphodrum* group. The series from Mt. Misim and that from the Snow Mts. agree almost perfectly in size, proportions, and structural details. The Snow Mts. specimens are a little darker, but the difference is slight and inconstant and may be due at least partly to methods of preservation: the Mt. Misim specimens, in alcohol; the Snow Mts. ones, apparently dry.

ALTAGONUM SPHODRUM n. sp.

Description. With characters of genus as described above. Form of a rather slender, large-headed sphodrine; piceous, appendages brownish, lateral margins of prothorax and elytra scarcely translucent; upper surface virtually impunctate, only moderately shining, not iridescent; microsculpture normal. *Head* large, appearing almost wide as prothorax but actually .82 & .81 as wide; eyes reduced, only moderately prominent; genae about as long as eyes, oblique, straight or slightly convex in profile; posterior supraocular setae behind line of posterior edges of eyes; neck-constriction distinct, moderately impressed; front irregularly convex, with moderate anterior impressions. *Prothorax* subquadrate; width/length 1.18 & 1.20; base/apex 1.28 & 1.20; sides weakly arcuate anteriorly, broadly sinuate well before basal angles; latter right-acute, accurately formed; lateral margins rather wide (in genus), moderately reflexed (outer edges more so than margins as wholes); posterior-lateral setae on edges of margins almost at basal angles; basal foveae rather shallow and poorly defined, a little roughened but not punctate; disc rather flat; middle line and transverse impressions poorly impressed; anterior and posterior marginal lines variable, not well impressed. *Elytra* rather narrow and long, otherwise about normal in form and convexity, not or only faintly impressed before middle; basal margin rather strongly but a little obtusely angulate at humeri; lateral margins rather narrow; subapical sinuations very slight; apices independently rounded, with sutural angles variable, sometimes rounded, sometimes obtuse and vaguely denticulate; striae moderately impressed, impunctate; intervals slightly convex, 7th and 8th toward apex and 9th for much of length more or less impressed longitudinally, 3rd usually normally 3-punctate (but only 2-punctate on left elytron of type). *Lower surface* roughened but virtually impunctate, except abdomen with fine punctation and extensive but inconspicuous pubescence. *Legs:* 4th hind-tarsal segment simply emarginate not lobed but with outer apical angle slightly more prominent than inner one; claws simple (not modified as in many true sphodrines). *Male copulatory organs:* Fig. 49. *Measurements:* length 10.5–12.0; width 3.4–4.1 (types only).

Types. Holotype ♂ (M.C.Z. No. 28,653) and 2 ♀♀ paratypes from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, 7,000–10,000 ft., Oct. 1944 (Darlington), under cover on the ground in heavy forest.

Other material. Besides the types I have a fourth (♀) specimen from the same locality which is larger (13.1 by 4.7 mm.), with somewhat more prominent eyes and relatively wider prothorax (width/length 1.29). This specimen is probably referable to *sphodrum,* but I have not included it in the type series.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This species is very distinct from any of the preceding ones in form and other characters. It has, however, two apparent relatives, treated below. In describing them I have taken *sphodrum* as the base-species for comparison.

ALTAGONUM POSTSULCATUM n. sp.

Description. With characters of genus as described above. Apparently closely related to the preceding (*sphodrum*) and answering to the same description (see above) in all details except those noted below. Form more *Calathus*-like than sphodrine; color about as in *sphodrum* except elytra more shining or even faintly iridescent in strong light; microsculpture same except finer and more transverse on elytra. *Head* relatively narrower than in *sphodrum*, .77 and .76 width prothorax, but with larger and more prominent eyes and short, oblique genae; posterior supraocular setae only slightly if at all behind line of posterior edges of eyes. *Prothorax* much more narrowed in front; width/length 1.30 & 1.38; base/apex 1.40 & 1.43; sides weakly arcuate, straight and slightly or scarcely converging and usually slightly sinuate toward base; basal angles right or slightly obtuse; disc normal; anterior and posterior marginal lines entire. *Elytra* slightly broader than in *sphodrum*, sometimes more distinctly impressed before middle; apices usually vaguely or distinctly denticulate; outer intervals impressed about as in *sphodrum*. *Lower surface* less roughened than in *sphodrum* and abdomen less extensively pubescent, but still plainly so especially near middle basally. *Legs:* 4th hind-tarsal segment emarginate. *Measurements:* length 9.0–9.9; width 3.3–3.7 mm.

Types. Holotype ♂ (Leiden Mus.) and 9 paratypes (some in M.C.Z. No. 28,654) from Mist Camp, Snow Mts., **Neth. N. G.**, 1,800 m. (about 5,850 ft.), Jan. (some paratypes Dec. 30, 1938, & Jan. 7 & 9) 1939 (Toxopeus); and the following additional paratypes all from the Snow Mts.; 5, Sigi Camp, 1,500 m. (about 4,875 ft.), Feb. (including Feb. 19 & 25) 1939; 1, mountain slope above Bernhard Camp, 1,700 m. (about 5,525 ft.), Jan. 7, 1939; 1, Top Camp, 2,100 m. (about 6,825 ft.), Feb. 8, 1939; and 4, Ibele (Iebele) Camp, 2,250 m. (about 7,325 ft.), Nov. & Nov.–Dec. 1939 (all specimens collected by Toxopeus).

Other material. One ♀ from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, 7,000–10,000 ft., Oct. 1944 (Darlington), in forest. This specimen differs slightly from the types in form and has the elytra a little less shining, with less strongly transverse microsculpture, but these and other differences are so small that I do not care to make them the basis of even a new subspecies without more material. The proportions of this specimen are: head/prothorax .73; prothoracic width/length 1.36; base/apex 1.38. Its length is 10.0 mm.

Measured specimens. Holotype ♂ and 1 ♀ paratype from Mist Camp.

Notes. This species is adequately distinguished from *sphodrum* and others in the key to species of *Altagonum,* above.

ALTAGONUM MISIM n. sp.

Description. With characters of genus as described above. Probably related to *sphodrum*; differing from latter in many details, but described partly by comparison in order to stress both similarities and differences. Form only vaguely sphodrine, more *Colpodes*-like; color, and sculpture of upper surface about as in *sphodrum. Head* smaller but with much larger eyes; .79 & .73 width prothorax; eyes large, prominent, with posterior supraocular setae before line of their posterior edges; neck-constriction scarcely indicated; front normally convex, with rather slight anterior impressions. *Prothorax* wider and relatively more narrowed in front than in *sphodrum*; width/length 1.36 & 1.44; base/apex 1.44 & 1.47; sides moderately arcuate for much of length, more or less strongly sinuate near base; basal angles right; lateral margins moderate, wider basally, moderately reflexed; posterior-lateral setae as in *sphodrum*; basal foveae deeper than in *sphodrum,* indistinctly punctate; disc normal; anterior and posterior marginal lines entire, well impressed. *Elytra* long and rather ample, a little less convex than usual, slightly impressed before middle; basal margin obtusely angulate or subangulate at humeri; lateral margins rather narrow; subapical sinuations moderate; apices somewhat produced, each with a short tooth or abrupt angulation about opposite 3rd interval and a stronger tooth (almost a short spine) at sutural angle; striae and intervals about as in *sphodrum,* with outer intervals impressed in about same way. *Lower surface* virtually impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment simply emarginate, as in *sphodrum. Measurements:* length 12.4–13.7; width 4.2–5.0 mm.

Types. Holotype ♀ (M.C.Z. No. 28,655) and 1 ♀ paratype from Mt. Misim, Morobe Dist., **N-E. N. G.**, the type specifically from 6,400 ft., Mar. (Stevens).

Measured specimens. The types.

Notes. This species probably belongs near *sphodrum* and *postsulcatum* (above) because of the impressed outer elytral intervals and form of prothorax, which agrees closely with that of *postsulcatum* though not of *sphodrum* itself, but *misim* differs from both these species in having elytra armed at apex and abdomen not pubescent, as well as in other less significant details: larger eyes, virtually no neck-constriction, etc.

ALTAGONUM CHEESMANI n. sp.

Description. With characters of genus as described above. Rather large, rather slender, subfusiform; black, elytra (except suture) green, appendages yellowish- or brownish-red, lateral margins of prothorax yellowish-translucent; upper surface impunctate except slightly punctate in basal foveae and marginal gutters of pronotum, moderately shining, not iridescent; microsculpture of head and pronotal disc not visible at 54×, of elytra distinct and transverse. *Head* .80 width pronotum; eyes large and very prominent, with posterior supraocular setae slightly before line of their posterior edges; neck-constriction slight and not well defined; front slightly convex, with moderate anterior impressions. *Prothorax* widest about middle, strongly narrowed in front, only slightly so behind; width/length 1.27; base/apex 1.69; anterior angles not at all advanced, so front of prothorax almost evenly truncate; sides moderately rounded for much of length, slightly sinuate toward base; basal angles right-obtuse, blunted; lateral margins rather wide but not well defined, slightly reflexed anteriorly, rather strongly so posteriorly; posterior-lateral setae on edges of margins at posterior angles; basal foveae deep, slightly punctate; disc normal, with light middle line and rather deep transverse impressions; anterior and posterior marginal lines fine but entire. *Elytra* long, subparallel for much of length, more convex than usual, not impressed on disc; basal margin obtusely angulate at humeri; lateral margins narrow; subapical sinuations moderate, broad, each leading onto a short, strong spine opposite 3rd interval; apices inside of spines strongly emarginate; sutural angles denticulate; striae light, punctulate; intervals flat, 8th and 9th not much modified toward apex, 3rd normally 3-punctate. *Lower surface* distinctly punctate only at sides of mesosternum; abdomen not pubescent. *Legs:* 4th hind-tarsal segment rather deeply emarginate, almost lobed, but outer angle or lobe not obviously longer than inner. *Measurements:* length 13.1; width 4.3 mm.

Type. Holotype ♀ (British Mus.) from Mafulu, **Papua**, 4,000 ft., Jan. 1934 (Cheesman); unique.

Measured specimen. The type.

Notes. This species, although placed among others in the key to species of *Altagonum* (above), is quite unlike any other known to me. It may be independently derived from *Colpodes.* It is more fusiform than any *Colpodes* known from New Guinea, however, and of course it lacks the anterior-lateral pronotal setae. It is a fine species, and I take great pleasure in naming it for Miss L. Evelyn Cheesman, who collected it and so many other interesting Carabidae in New Guinea.

ALTAGONUM SCAPHA n. sp.

Description. With characters of genus as described above. Rather small, slender, fusiform; brownish-black, legs only slightly paler, antennae yellowish, sides and sometimes base of prothorax narrowly, vaguely paler; upper surface impunctate, moderately shining, not distinctly iridescent; microsculpture normal but light. *Head* narrow, .65, .62, & .63 width prothorax; eyes large but less convex than usual, not very prominent, with posterior supraocular setae about between their posterior edges; neck constriction vague; front normal. *Prothorax* much narrowed in front, scarcely at all so behind; width/length 1.24, 1.28, & 1.29; base/apex 1.67, 1.80, & 1.70; anterior angles scarcely advanced; sides moderately arcuate anteriorly, nearly straight posteriorly, not distinctly sinuate; basal angles almost right except narrowly rounded; lateral margins narrow, scarcely reflexed; posterior-lateral setae on flat surface a little in from edges of margins near basal angles; basal foveae slight, almost obsolete; disc only weakly convex, with median line and transverse impressions weak; anterior and posterior marginal lines light or interrupted at middle. *Elytra* elongate-oval, more pointed behind and more convex than usual; basal margin about rectangular at humeri; lateral margins narrow; subapical sinuations variable, present only when elytra spined; apices each with a short spine or acute angulation opposite 3rd interval, then oblique forward and more or less emarginate to more or less strongly denticulate sutural angles; striae rather lightly impressed, not punctate; intervals flat or slightly convex, 8th and 9th not much modified toward apex, 3rd 2-punctate (anterior puncture absent on both sides in all specimens). *Lower surface* impunctate; abdomen not pubescent; prosternal process simple or vaguely margined at apex. *Legs:* hind tarsi very slender; 4th hind-tarsal segment emarginate or with very short lobes, with outer angle always a little longer than inner. *Measurements* (types): length 7.2–8.0; width 2.6–2.9 mm.

Types. Holotype ♂ (Leiden Mus.) from Rattan Camp, Snow Mts., **Neth. N. G.**, 1,150 m. (about 3,750 ft.), Feb.–Mar. 1939 (Toxopeus); 1 ♂ paratype (M.C.Z. No. 28,656) from Top Camp, Snow Mts., 2,100 m. (about 6,825 ft.), Jan. 22, 1939 (Toxopeus); 1 ♀ paratype (British Mus.) from Camp Nok, Waigeo Is., 2,500 ft., Apr. 1938 (Cheesman).

Other material. The type of *scapha* has the elytra spined; the ♂ paratype, acutely angulate. The ♀ paratype from Waigeo Is. has them spined and matches the type in all other significant non-sexual characters. I have examined also 2 additional, larger specimens from the Snow Mts. In one, a ♂ from Ibele (Iebele) Camp, 2,250 m. (about 7,325 ft.), Nov. 1938 (Toxopeus), the apical angulations of the elytra are slightly obtuse rather than acute, less prominent even than in the ♂ paratype, and the proportions are head .61 width prothorax, prothoracic width/length 1.15 and base/apex 1.81, and length 9.3, width 3.1 mm. In this ♂ and in the 2 ♂♂ types the apex of the aedeagus is recurved or barbed below, the exact form being a little different in each specimen, but within the possible range of variation of a species. The final specimen is a ♀ from Mist Camp, 1,800 m. (about 5,850 ft.), Jan. 1939 (Toxopeus). It has the elytra spined as in the type, but it differs slightly in proportions and is much larger: head .57 width prothorax, prothoracic width/length 1.26, base/apex 1.73, length 11.3, width 4.0 mm. The significance of these variations cannot be determined without more material.

Measured specimens. The 3 types.

Notes. This species is sufficiently compared with others in the key to species of *Altagonum*, above.

ALTAGONUM REGISCAPHA n. sp.

Description. With characters of genus as described above. Similar to *scapha*, to the description of which (see above) it answers in all details except those noted below. Broader than *scapha*; elytra inconspicuously purple with greenish reflections, legs dark reddish; microsculpture of head and pronotum so light as to be scarcely visible. *Head* with eyes somewhat more prominent than in *scapha*, .65 width prothorax. *Prothorax* relatively wider but otherwise similarly formed; width/length 1.36; base/apex 1.78; basal angles slightly more obtuse; lateral margins wider; posterior-lateral setae virtually on (not well inside of) edges of margins at basal angles; basal foveae more distinct, broad, but still shallow and poorly defined. *Elytra* slightly broader and less pointed behind; subapical sinuations virtually absent; apices rectangular about opposite 3rd intervals, then oblique forward to slightly denticulate sutural angles; 3rd interval 2-punctate as in *scapha*. *Legs:* 4th hind-tarsal segment simply emarginate, not lobed. *Measurements:* length 9.1; width 3.4 mm.

Type. Holotype ♀ (Leiden Mus.) from Mist Camp, Snow Mts., **Neth. N. G.**, 1,800 m. (about 5,850 ft.), Jan. 1939 (Toxopeus); unique.

Measured specimen. The type.

Notes. This species is very similar to *scapha*, but whether it is an actual relative or a convergent form I do not know. The difference in position of the posterior-lateral setae and the somewhat different form of the 4th hind-tarsal segment suggest that the relationship may not be very close.

ALTAGONUM LATILIMBUS n. sp.

Description. With characters of genus as described above. Form of rather broad *Calathus*; brownish-black, broadly margined with yellow (yellow covers actual margins of prothorax, margins and about 3 outer intervals in basal half of elytra, and a still wider zone posteriorly, including elytral apices; boundary of dark discal area fairly regular, dark color not forming a narrow sutural stripe toward apex), sides and apex of abdomen narrowly margined or spotted with yellow, appendages yellow; upper surface impunctate, only moderately shining, not distinctly iridescent; microsculpture normal. *Head* small, .57 & .56 width prothorax; eyes moderately large and prominent, with posterior supraocular setae about between their posterior edges; neck not constricted above; front weakly convex, with weak anterior impressions. *Prothorax* rather broad, much narrowed in front, scarcely or not narrowed behind; width/length 1.48 & 1.44; base/apex 1.61 & 1.59; anterior angles broadly and rather strongly advanced, subacute except narrowly rounded; sides weakly arcuate for much of length, almost straight and sometimes very slightly sinuate posteriorly; basal angles subrectangular except very narrowly rounded; lateral margins narrow anteriorly, wide and flat posteriorly; posterior-lateral setae on flat surfaces of margins about equally distant from inner and outer edges and base, or nearer inner edges; basal foveae almost obsolete, not distinct from flattened margins, not or at most vaguely punctate; disc moderately convex, with middle line and transverse impressions slight; anterior marginal line entire, posterior one faint or interrupted at middle. *Elytra* nearly normal in outline and only slightly more convex than usual, with disc not or faintly impressed; basal margin almost rectangular at humeri (but points of angles blunted); lateral margins average; subapical sinuations very slight; apices simple, with sutural angles obtuse, not or faintly denticulate; striae rather lightly impressed, impunctate; intervals nearly flat or slightly convex, 8th and 9th not much modified toward apex, 3rd normally 3-punctate. *Lower surface* impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment emarginate, not lobed. *Measurements:* length 8.5–8.9; width 3.4–3.5 mm.

Types. Holotype ♂ (Leiden Mus.) and 2 ♂♂ paratypes (1 in M.C.Z. No. 28,657) from Mist Camp, Snow Mts., **Neth. N. G.,** 1,800 m. (about 5,850 ft.), Jan. (the paratypes Jan. 9 & 11) 1939;

1 ♂ paratype from Sigi Camp, Snow Mts., 1,500 m. (about 4,875 ft.), Feb. 25, 1939; and 1 ♂ paratype and hind-body of another specimen from Top Camp, Snow Mts., 2,100 m. (about 6,825 ft.), Jan. 27 & Feb. 8, 1939; (all specimens collected by Toxopeus).

Measured specimens. The ♂ holotype and 1 ♂ paratype from Mist Camp.

Notes. So far as I know, this species has only one close relative, described below. It may be more distantly related to *scapha* (above), which also is fusiform, with posterior pronotal setae somewhat removed from the edges of the margins, but *latilimbus* is very different from *scapha* in coloration, strongly advanced anterior prothoracic angles, simple elytral apices, and other details.

ALTAGONUM PARALIMBUS n. sp.

Description. Very close to *latilimbus*, to the description of which (see above) it answers in all details not noted below. Slightly narrower than *latilimbus*; yellow margins of elytra narrower anteriorly (including only about 2 intervals), broad but irregularly limited posteriorly, with dark discal color extending along sutural intervals toward (but not to) apex; surface a little more shining than in *latilimbus*. *Head* .57 & .57 width prothorax; eyes slightly less prominent than in *latilimbus*. *Prothorax:* width/length 1.32 & 1.34; base/apex 1.51 & 1.48. *Elytra* with disc a little more distinctly impressed slightly before middle than in *latilimbus*. *Male copulatory organs:* Fig. 50. *Measurements:* length 9.9–10.2; width 3.7–3.8 mm.

Types. Holotype ♂ (M.C.Z. No. 28,658) from Mt. Misim, Morobe Dist., **N-E. N. G.** (Stevens); and 1 ♀ paratype (British Mus.) from Mt. Tafa, **Papua**, 8,500 ft., Mar. 1934 (Cheesman).

Measured specimens. The types.

Notes. As compared with *latilimbus*, this differs chiefly in its more slender form and more irregular boundary of dark and light areas toward apex of elytra.

ALTAGONUM NUDICOLLE n. sp.

Description. With characters of genus as described above. Form of rather broad *Calathus*; dark-brown or brownish-black, legs not much paler, antennae a little redder, lateral margins of prothorax slightly reddish-translucent; surface not very shining, not iridescent; microsculpture very distinct, normal except meshes less transverse than usual on elytra. *Head* .67 & .64 width prothorax; eyes moderately large and prominent, with posterior supraocular setae about between their posterior edges; neck slightly impressed above; front somewhat irregularly convex, with slight anterior impressions. *Prothorax* widest near middle, strongly narrowed anteriorly, scarcely if at all so posteriorly; width/length 1.33 & 1.35; base/apex 1.65 & 1.64; anterior angles moderately advanced, would be right or slightly acute except narrowly rounded; sides arcuate for much of length, then straight or slightly and broadly sinuate before base; posterior angles approximately right, scarcely blunted; lateral margins rather wide especially toward base but only moderately reflexed; both pairs (posterior as well as anterior) lateral setae absent; basal foveae slight, scarcely distinct from ends of lateral margins, impunctate; disc less convex than usual; anterior marginal line entire, posterior one usually entire but sometimes vague at middle. *Elytra* rather broad and ample, nearly normal in outline but more convex than usual; basal margin rectangular at humeri; lateral margins narrow; subapical sinuations slight or nearly absent; apices rather narrowly rounded; sutural angles obtuse or rounded, not denticulate; striae lightly impressed, not punctate; intervals flat or nearly so, more or less vaguely longitudinally impressed at extreme apices, but 9th not or only vaguely impressed, 3rd normally 3-punctate. *Lower surface* impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment with short outer and still shorter inner lobe. *Male copulatory organs:* Fig. 51. *Measurements:* length 11.2–12.3; width 4.3–5.1 mm.

Types. Holotype ♂ (M.C.Z. No. 28,659) and 67 paratypes all from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, 7,000–10,000 ft., Oct. 1949 (Darlington), in and under various ground-cover in forest.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. The slight impression of the elytral intervals and some other details suggest that this species may be related to *sphodrum* and *postsulcatum* (above), but it is much broader, without abdominal pubescence, and has lost the posterior- as well as the anterior-lateral pronotal setae.

ALTAGONUM FATUUM n. sp.

Description. With characters of genus as described above. Form nearly that of slender *Platynus,* with slender appendages; brownish-black, elytra browner, appendages yellow, lateral margins of prothorax and elytra yellow-translucent, epipleurae yellow, sides and apex of abdomen broadly yellow; upper surface virtually impunctate, moderately shining, not iridescent; microsculpture normal, distinct. *Head* rather long, .74 & .72 width prothorax; eyes slightly reduced, only moderately prominent; genae about half as long as eyes, oblique;

posterior supraocular setae slightly behind line of posterior edges of eyes; neck slightly impressed above; front normal. *Prothorax* rather narrow, subquadrate, moderately narrowed anteriorly, only slightly so posteriorly; width/length 1.09 & 1.14; base/apex 1.40 & 1.43; anterior angles scarcely advanced; sides rather weakly arcuate for much of length, more or less straight and sometimes faintly sinuate toward base; posterior angles rather narrowly rounded; lateral margins rather narrow, only a little wider toward base, moderately reflexed; both pairs lateral pronotal setae absent; basal foveae normal, a little irregular at bottom but not distinctly punctate; disc normal; anterior and posterior marginal lines entire. *Elytra* long but otherwise of nearly normal outline, slightly more convex than usual, with disc not impressed; basal margin distinctly but somewhat obtusely angulate at humeri; lateral margins narrow; subapical sinuations faint or absent; apices moderately rounded to suture; sutural angles not or faintly denticulate; striae moderately impressed, not punctate; intervals nearly flat or slightly convex, 8th and 9th not much modified toward apex, 3rd impunctate. *Lower surface* impunctate; abdomen not pubescent. *Legs:* 4th hind-tarsal segment emarginate, not lobed. *Measurements:* length 10.0–10.3; width 3.6–3.9 mm.

Types. Holotype ♂ (British Mus.) and 2 (♂ ♀) paratypes (♂ in M.C.Z. No. 28,660) all from Mt. Tafa, **Papua**, 8,500 ft., Mar. 1934 (Cheesman).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This species, although placed in the key to species of *Altagonum* (above), is very different from any other known to me.

MACULAGONUM new genus

Diagnosis. Rather small (5.7 to 8.9 mm), either narrow *Agonum*-like or more or less fusiform; elytra always mottled or blotched with dark and pale; wing-and-seta formula +w, ++, (−)+, −(+)+; last ventral abdominal segment of ♂ rather deeply notched at middle of apex; genus otherwise within range of variation of *Altagonum* (above).

Description. Form and color as indicated above; upper surface impunctate (except in *setipox*), more or less shining, not iridescent; microsculpture variable. *Head* moderate or small, usually rather short (in tribe), sometimes slightly elongate; neck more or less impressed above except in *scaphipox*; eyes variable, either large, or slightly reduced in size and prominence, or small but abruptly prominent; both pairs supraocular setae present; antennae normal; mentum tooth triangular. *Prothorax* somewhat variable, more or less strongly narrowed in front (least so in *pox*), with anterior angles not advanced, more or less rounded out; anterior-lateral setae absent (except in *setipox*), posterior-lateral ones present on or just within basal angles. *Elytra* long and/or ample, more convex than usual; disc not distinctly impressed; basal margin entire, variably angulate at humeri; apices variable but never spined nor abruptly angulate; intervals not much modified toward apex (except 8th more convex than usual toward apex in *scaphipox*); 3rd interval 2- or 1-punctate (anterior and sometimes middle puncture absent). *Inner wings* full. *Lower surface* impunctate; abdomen not pubescent; prosternal process simple. *Legs:* hind tibiae not sulcate along outer edges; 4th hind-tarsal segment emarginate, not lobed; 5th hind-tarsal segment without obvious accessory setae; claws simple. *Secondary sexual characters* normal except last ventral abdominal segment more or less deeply notched at middle of apex in ♂, though not in ♀. *Male copulatory organs* as figured (Fig. 52).

Genotype. *Maculagonum pox* n. sp. (below).

Generic distribution. Mountains of New Guinea.

Notes. Of the six species of this new genus, I have seen males of only four, but the four include the extremes of generic variation in most other characters. All these males have the last ventral segment more deeply and abruptly emarginate than males of any *Altagonum* that I have been able to examine (as a rule the male last ventral is entire in *Altagonum*, but it is slightly emarginate in *scapha* and sometimes in *vallicola* and perhaps in other species). I think that this character will probably be found to hold for males of all species of *Maculagonum*. The mottling or blotching of the elytra is the most obvious character of this genus. It may be an adaptation to life in grass, tending to conceal the insects in finely divided light and shade. At least the only specimen of the genus that I have collected (the type of *altipox*) was found in a tussock on a grassy slope above timber line on Mt. Wilhelm. Some of the specimens of *Maculagonum* collected by Cheesman and Toxopeus were probably taken in light traps, for they have scales of Lepidoptera stuck to them.

Key to the Species of Maculagonum

1. Lateral margins of prothorax moderately wide; length 8.2 to 8.9 mm....2
– Lateral margins of prothorax very narrow; length 5.7 to 7.7 mm........3
2. Elytra finely mottled with dark and pale (p. 215).................. *pox*
– Elytra dark with a large common pale blotch before middle and another about ¼ from apex (p. 216)................................ *plagipox*
3. Anterior-lateral as well as posterior-lateral pronotal setae present; eyes small but abnormally prominent (p. 217)..................... *setipox*

– Anterior-lateral pronotal setae absent; eyes larger but only moderately prominent 4

4. Apices of elytra more broadly and evenly rounded; elytral microsculpture deeply impressed, isodiametric . . . . *altipox*
   - (4a) Darker, with dark areas of elytra more extensive and blackish or dark-brown (p. 218) . . . . (*altipox s. s.*)
   - (4b) Paler, with dark areas of elytra less extensive and paler brown; (see also description) (p. 219) . . . . (subsp. *pallipox*)

– Apices of elytra more narrowly and abruptly rounded (lobed) about opposite 4th intervals; elytral microsculpture less deep, somewhat transverse . . . 5

5. Slender, not fusiform; prothoracic width/length 1.19; 3rd elytral interval 1-punctate (p. 219) . . . . *tafapox*

– Fusiform; prothoracic width/length 1.46; 3rd elytral interval 2-punctate (p. 220) . . . . *scaphipox*

MACULAGONUM POX n. sp.

Description. With characters of genus as described above. Form (Fig. 7) somewhat *Agonum*-like, but more elongate-oval than usual in *Agonum s. s.*; more or less dark-brown, lateral margins of prothorax yellow-translucent, elytra mottled with small yellowish spots which sometimes form rows along intervals or sometimes anastomose, appendages yellowish-brown; microsculpture nearly normal but faint on head and pronotum, more distinct and only moderately transverse on elytra. *Head* .74 & .72 width prothorax; eyes large and prominent, with posterior supraocular setae about between their posterior edges; front convex, with usual slight anterior impressions and often (not always) also with an extra impression each side near eye, behind and inside of anterior supraocular seta. *Prothorax* of moderate size, much narrowed in front and moderately so behind; width/length 1.35 & 1.40; base/apex about 1.60 (angles too rounded for accurate measurement); sides nearly evenly rounded for all or most of length, sometimes more or less straight but hardly sinuate toward base; posterior angles obtuse, blunted or narrowly rounded; lateral margins moderately wide, wider toward base, only slightly reflexed; basal foveae roundish, shallow, impunctate; disc normal; anterior and posterior marginal lines light, sometimes interrupted at middle. *Elytra* rather long; basal margin rather strongly but somewhat obtusely angulate at humeri; lateral margins narrow; subapical sinuations obsolete or nearly so; apices rather strongly rounded about opposite 3rd intervals, then oblique forward and obtusely angulate or subdenticulate at suture; striae rather lightly impressed, impunctate (sometimes appearing punctate in soft specimens); intervals flat or slightly convex, 3rd 2-punctate. *Secondary sexual characters* normal except last ventral abdominal

segment of ♂ abruptly notched at middle of apex (bottom of notch would be right or slightly acute if not narrowly rounded), of ♀ entire. *Measurements:* length 8.2–8.9; width 3.1–3.3 mm.

Types. Holotype ♀ (Leiden Mus.) and 1 ♂ 3 ♀♀ paratypes (2 ♀♀ in M.C.Z. No. 28,661) from Sigi Camp, Snow Mts., **Neth. N. G.**, 1,500 m. (about 4,875 ft.), Feb. 17 (holotype), 19, & 25, 1939 (Toxopeus); and 1 ♀ paratype from Mist Camp, Snow Mts., 1,800 m. (about 5,850 ft.), Jan. 9, 1939 (Toxopeus).

Measured specimens. The ♀ holotype and ♂ paratype.

Notes. This species is sufficiently compared with others in the key, above. The single ♂ and 3 of the 4 ♀♀ paratypes are so soft that their elytra have crumpled or are at least not well formed. The copulatory organs of the ♂ are too unformed to draw.

MACULAGONUM PLAGIPOX n. sp.

Description. With characters of genus as described above. A little more slender than *pox*; color (of single, soft specimen) brown; lateral margins of prothorax yellow-translucent; elytra with 2 common, transversely oval, pale plagiae involving the 4 inner intervals of each elytron, centering slightly before middle of elytral length and about ¼ from apex; appendages yellow; microsculpture absent or very faint on head and pronotum, moderately transverse on elytra. *Head* .77 width prothorax; eyes large and prominent, with posterior supraocular setae about between their posterior edges; front broadly impressed each side from behind anterior supraocular seta to clypeal suture (but impressions may be due to warping of soft integument). *Prothorax* a little longer and less narrowed behind than in *pox*; width/length 1.23; base/apex about 1.63; sides rather weakly arcuate anteriorly, nearly straight and scarcely converging behind middle; posterior angles a little obtuse and rather narrowly rounded; lateral margins moderate, wider toward base, only slightly reflexed; anterior and posterior marginal lines entire. *Elytra* warped, long but apparently of nearly normal outline; basal margin obtusely subangulate at humeri; lateral margins wider than in *pox*; apices apparently formed as in *pox*; striae appear rather deeply impressed and somewhat punctate, but might be lighter and impunctate in fully hardened specimens; intervals abnormally warped in single specimen, 3rd 2-punctate. *Legs:* 4 outer segments of both hind tarsi missing, but structure presumably as in other species of genus. *Secondary sexual characters:* last ventral segment of ♂ notched as in *pox*. *Measurements:* length 8.6; width probably about 3.0 mm.

Type. Holotype ♂ (British Mus.) from Cyclops Mts., **Neth. N. G.**, 3,500 ft., Mar. 1936 (Cheesman); unique.

Measured specimen. The type.

Notes. Although this species is represented by a single soft and somewhat warped specimen, and although it is structurally fairly close to *pox*, I have no doubt it is distinct. It differs from *pox* not only in color-pattern but also in form especially of the prothorax, and in greater width of the elytral margins. I have not wanted to risk remounting the single soft specimen, which is glued to a small card, and so have been unable to examine the lower surface except from the side. Fortunately the form of the apex of the last ventral segment can be seen from above. Also, I have not risked dissecting out the genitalia, which would probably be too unformed for study in any case.

MACULAGONUM SETIPOX n. sp.

Description. With characters of genus as described above. Half-fusiform, more than usually tapering anteriorly but not posteriorly; brownish-piceous with slight aeneous lustre; lateral margins of prothorax somewhat translucent posteriorly only; elytra mottled with paler brown, many of the pale marks confined to single intervals, others coalescing to form irregular blotches; appendages yellowish; microsculpture faint on head and pronotum, deeply impressed and isodiametric on elytra. *Head* .78 width prothorax; eyes rather small but abruptly prominent, with posterior supraocular setae far behind line of their posterior margins; vertex somewhat swollen; front broadly, slightly, transversely impressed between eyes, and with a long anterior impression extending from above each eye to base of clypeus. *Prothorax* broadest at extreme base; width/length 1.10; base/apex about 1.67; sides weakly arcuate anteriorly, straight and slightly diverging in posterior half; posterior angles right, well defined; base slightly lobed at middle, slightly oblique at sides to angles; lateral margins very narrow, each with a short seta before middle as well as one at basal angle; basal foveae rather shallow and poorly defined, they and adjacent areas of pronotum punctate; disc more wrinkled (transversely) than usual, otherwise normal; anterior and posterior marginal lines entire. *Elytra* with basal margin obtusely subangulate at humeri; lateral margins narrow; subapical sinuations slight; apices beyond sinuations nearly evenly, subindependently rounded to obtuse, slightly blunted sutural angles; striae shallow, vaguely punctulate; intervals flat, 3rd 2-punctate. *Secondary sexual characters:* last ventral abdominal segment of ♂ emarginate at middle of apex, with bottom of emargination almost rectangular. *Male copulatory organs:* Fig. 52. *Measurements:* length 7.7; width 2.9 mm.

Type. Holotype ♂ (British Mus.) from Mt. Tafa, **Papua**, 8,500 ft., Feb. 1934 (Cheesman); unique.

Measured specimen. The type.

Notes. This is an exceptionally distinct species, unique within the genus in form, form of eyes, impressions of front, presence of both pairs of lateral pronotal setae, and punctation and extra wrinkling of pronotum.

Maculagonum altipox n. sp.

Description. With characters of genus as described above. Form intermediate, between normal *Agonum*-like and (anteriorly) subfusiform; dark-brown, pronotum with anterior and lateral margins narrowly and base widely yellow, the latter finely speckled with dark; elytra mottled with many small yellow spots, the larger ones very irregular in outline, forming rows along intervals, and anastomosing very little; appendages pale, except antennal segments 2 to 4 infuscate basally; microsculpture light but normal on head and pronotum, deeply impressed and isodiametric on elytra. *Head* .76 width prothorax; eyes only slightly shorter but less prominent than in *pox*, with posterior supraocular setae slightly behind line of their posterior edges; neck only slightly impressed above; front convex, with only slight and irregular anterior impressions. *Prothorax* small, widest in basal half, slightly tapering anteriorly; width/length 1.28; base/apex about 1.64; sides slightly arcuate anteriorly, almost straight and parallel in almost basal half; base broadly lobed at middle, somewhat oblique at sides; posterior angles slightly obtuse, slightly blunted; lateral margins very narrow; immediate baso-lateral areas (just inside angles) rather broadly swollen rather than depressed, not punctate, but basal area impressed each side inside of swelling; disc normal, but median line and transverse impressions slighter than usual; anterior and posterior marginal lines light, vague or interrupted at middle. *Elytra* relatively ample; basal margin obtusely angulate at humeri; lateral margins very narrow; subapical sinuations almost obsolete; apices broadly and almost conjointly rounded to obtuse sutural angles; striae light, not distinctly punctate; intervals flat or nearly so, 3rd 1-punctate. *Secondary sexual characters:* ♂ unknown; ♀ with last ventral abdominal segment broadly subtruncate, virtually entire. *Measurements:* length 7.0; width about 2.7 mm.

Type. Holotype ♀ (M.C.Z. No. 28,662) from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, over 10,000 ft. (on open grassy slope just above timber line), Oct. 1944 (Darlington).

Measured specimen. The type.

Notes. This species is sufficiently compared with others in the key to species of *Maculagonum,* above.

MACULAGONUM ALTIPOX PALLIPOX n. subsp.

Description. Similar to typical *altipox* but paler, with pale spots of elytra more extensive and tending to coalesce in certain areas, especially in a common sutural blotch about ¼ from apex, and along outer margins; microsculpture as in typical *altipox. Head* .79 & .80 width prothorax, formed about as in *altipox. Prothorax* almost as in *altipox* but slightly narrowed behind; width/length 1.24 & 1.27; base/apex about 1.50 & 1.57; baso-lateral areas only slightly swollen. *Elytra* about as in *altipox* but with apices more independently, less conjointly rounded; 3rd interval similarly 1-punctate. *Secondary sexual characters:* normal; and last ventral abdominal segment of ♂ moderately emarginate at apex, the bottom of the emargination obtuse; last ventral of ♀ subtruncate. *Measurements:* length 6.9–7.2; width about 2.8 mm.

Types. Holotype ♂ (Leiden Mus.) and 1 ♀ paratype (M.C.Z. No. 28,663) both from Moss Forest Camp, Snow Mts., **Neth. N. G.**, 2,800 m. (about 9,100 ft.), Oct. 9–Nov. 5, 1938 (Toxopeus).

Measured specimens. The types.

Notes. Sufficiently compared with typical *altipox* above. The two specimens of *pallipox* are not quite fully hardened, and this may affect the intensity of the color, but not the pattern. I have dissected out the genitalia of the ♂ type, but they are not hard enough to show characters properly.

MACULAGONUM TAFAPOX n. sp.

Description. With characters of genus as described above. Small and slender, almost *Europhilus*-like but more convex, with prothorax less narrowed behind and elytra more oval than usual in *Europhilus*; brown; prothorax with anterior margin less and sides and posterior margin more distinctly margined with yellow; elytra primarily yellowish with dark brown mottling especially on disc, and with dark marks coalescing to form an irregular blotch between 3rd and 7th striae about ⅓ from apex on each elytron; appendages yellowish except antennal segments 3, 4, and less distinctly 5 infuscate basally; microsculpture normal except only slightly transverse on elytra. *Head* .77 width prothorax; eyes somewhat smaller and much less prominent than in *pox,* but with posterior supraocular setae scarcely behind line of their posterior edges; otherwise about as in *pox*. *Prothorax* small, subquadrate except rather strongly narrowed near front; width/length 1.19; base/apex about 1.46; sides only moderately arcuate anteriorly, straight and slightly converging behind middle; posterior angles slightly obtuse, blunted or very narrowly rounded; lateral margins very narrow; basal foveae poorly defined and only slightly impressed, with surface slightly swollen just inside angles; disc normal; anterior and posterior marginal lines more or less entire but not well marked. *Elytra* elongate-oval; basal margin almost rectangular at humeri; lateral margins very narrow; subapical sinuations slight; apices rather strongly lobed about opposite 4th intervals, then oblique forward to obtuse sutural angles; striae well marked but only lightly impressed, not distinctly punctate; intervals flat or nearly so, 3rd 1-punctate. *Secondary sexual characters:* ♂ unknown, ♀ with last ventral abdominal segment entire. *Measurements:* length 5.7; width 2.0 mm.

Type. Holotype ♀ (British Mus.) from Mt. Tafa, **Papua**, 8,500 ft., Feb. 1934 (Cheesman); unique.

Measured specimen. The type.

Notes. This species is sufficiently differentiated from others in the key to species of *Maculagonum*.

MACULAGONUM SCAPHIPOX n. sp.

Description. With characters of genus as described above. Fusiform, convex; brownish-piceous; prothorax with anterior margin faintly and lateral and posterior margins more distinctly (but not strikingly) yellowish; elytra irregularly mottled with dark and yellowish, the dark color almost solid on anterior half of disc and near apices, the yellow color predominating in a submarginal zone in about anterior ⅔ of each elytron and in a small, irregular, common sutural blotch about ¼ from apex; legs inconspicuously bicolored, femora and tibiae darker at middle than at ends; antennae yellowish with bases of several segments (especially 2nd to 4th) infuscate; microsculpture normal, but only moderately transverse on elytra. *Head* .64 width prothorax; eyes of nearly normal length but much less prominent than in *pox*, with posterior supraocular setae about between their posterior edges; neck not impressed above; front more convex than usual, with slight anterior impressions. *Prothorax* wider than usual in genus, very strongly narrowed in front, scarcely so behind; width/length 1.46; base/apex about 1.82; sides moderately arcuate for most of length, almost straight just before base; basal angles slightly obtuse, slightly blunted; lateral margins very narrow; baso-lateral areas smoothly convex near angles, but basal area impressed each side almost as near to middle as to sides;

disc normal; anterior and posterior marginal lines entire but not deeply impressed. *Elytra* with basal margin about rectangular at humeri; lateral margins very narrow; subapical sinuations slight; apices strongly lobed about opposite 4th intervals, then oblique forward to obtuse, indistinctly denticulate sutural angles; striae better impressed than usual in genus, not distinctly punctate; intervals slightly convex, 8th narrow and much more convex toward apex, 3rd 2-punctate. *Secondary sexual characters* of ♂ unknown; ♀ with last ventral abdominal segment broadly subtruncate. *Measurements:* length 6.0; width 2.3 mm.

Type. Holotype ♀ (British Mus.) from Orrori, **Papua**, 3,500 ft., July 1933 (Cheesman); unique.

Measured specimen. The type.

Notes. This may be related to the preceding (*tafapox*) but differs in many characters, of which only a few of the more obvious are noted in the key to species of *Maculagonum.*

POTAMAGONUM new genus

Diagnosis. Based on one species, so generic and specific characters not separable, but genus characterized by large size (14–15.5 mm.); unusually long and slender appendages; wide, translucent prothoracic margin; conspicuously interrupted elytral striae; conspicuous accessory setae of 5th hind-tarsal segment; and wing-and-seta formula +w, ++, −−, +++.

Description. See that of genotype, below.

Genotype. *Potamagonum diaphanum* n. sp. (below).

Generic distribution. As yet known only from the Bismarck Range, N-E. New Guinea.

Notes. For comparison with other genera, see key to genera, above.

POTAMAGONUM DIAPHANUM n. sp.

Description. Form as figured (Fig. 8). Rather large, slender, with unusually long, slender appendages; castaneous, appendages not much paler, but tibiae paler than femora in some individuals; lateral margins of prothorax widely and conspicuously translucent; rows of pale or translucent spots along elytral striae in some individuals; shining; microsculpture of head and pronotum indistinct, of elytra light and moderately transverse. *Head* only moderately elongate (in tribe), .70 & .71 width prothorax; eyes rather large and prominent; both pairs supraocular setae present, posterior pair about between posterior edges of eyes; front normally convex, not wrinkled between eyes, impunctate, with slight frontal impressions; neck-constriction rather deep but not sharply defined; mentum tooth triangular, somewhat blunted or rounded at apex. *Prothorax* rounded except apex emarginate and base slightly convexly subtruncate; width/length 1.27 & 1.23; base/apex not determined because of broad rounding of both anterior and posterior angles; basal foveae small, deep, not distinguishable from ends of lateral margins, impunctate; disc of pronotum normally convex, with light median line and rather deep transverse impressions, impunctate; anterior and posterior marginal lines entire, deeply impressed. *Elytra* long, subparallel or slightly narrowed anteriorly, convex; basal margin entire, obtusely angulate at humeri; lateral margins very narrow; subapical sinuations moderate (variable), broad, leading onto acute angulations or short spines about opposite 4th intervals; apices then oblique forward and more or less emarginate to denticulate sutural angles; striation entire but striae conspicuously interrupted, reduced to series of short impressed lines; intervals approximately flat but very irregular, 8th and 9th not much modified toward apex, 3rd normally but inconspicuously 3-punctate. *Inner wings* fully developed. *Lower surface* impunctate; abdomen not pubescent; prosternal process simple; metepisterna long. *Legs* normally formed but slender; hind tibiae not sulcate along outer edges; hind tarsi slender, sulcate each side above; 4th hind-tarsal segment deeply emarginate and with short lobes, outer scarcely longer than inner; 5th hind-tarsal segment with a row of conspicuous accessory setae on each side below; claws simple. *Secondary sexual characters* normal. *Male copulatory organs* as figured (Fig. 53). *Measurements:* length about 14–15.5; width about 3.5 mm. or slightly more (elytra too warped and spread for accurate measurements).

Types. Holotype ♂ (M.C.Z. No. 28,664) and 8 paratypes all from Chimbu Valley (some specimens labeled Mt. Wilhelm), Bismarck Range, **N-E. N. G.**, 5,000–7,500 & 7,000–10,000 ft., Oct. 1944 (Darlington); all taken among wet stones and in other cover on the spray-drenched banks of the turbulent Chim River at various altitudes within the limits given.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This species has perhaps been derived from a *Colpodes*-like ancestor, but it seems distinct enough to stand as a separate genus endemic to the high mountains of New Guinea.

GASTRAGONUM new genus

Diagnosis. In most ways similar to *Notagonum* but more convex, with eyes always so reduced that posterior supraocular setae are well behind line of their posterior edges, and often with wings reduced too;

small (5.8–8.3 mm.), *Gastrellarius*- or broad *Stenolophus*- or even *Trechus*-like forms; brown or piceous, elytra sometimes slightly iridescent, appendages somewhat but usually not strikingly paler; wing-and-seta formula ±w, ++, ++, +++.

Description. Form and color as described above; microsculpture variable, rarely absent. *Head* about as in *Notagonum*, except for reduction of eyes; both pairs supraocular setae always present; antennae a little shorter than usual in *Notagonum* but normally formed; frontal impressions variable; mentum tooth somewhat variable, often shorter or shorter and wider than usual in *Notagonum*. *Prothorax* usually more convex, but otherwise as in *Notagonum*, with both pairs lateral pronotal setae always present. *Elytra* also more convex than usual but otherwise within common range of variation of *Notagonum*; apices always simple, with sutural angles not denticulate; outer intervals never much modified toward apex; 3rd interval always normally 3-punctate. *Inner wings* full, dimorphic, or vestigial. *Lower surface* as usual in *Notagonum*, not or only locally and slightly punctate; abdomen rarely pubescent, usually not; prosternal process simple; metepisterna variable, shortened in some species with reduced wings. *Legs* as in *Notagonum*; hind tarsi moderately slender, slightly or not distinctly sulcate at sides above; 4th hind-tarsal segment different in different species; 5th hind-tarsal segment without obvious accessory setae; claws simple. *Secondary sexual characters* as in *Notagonum* (normal). *Male copulatory organs* simply agonine (Figs. 54–56).

Genotype. *Gastragonum terrestre* n. sp. (below).

Generic distribution. Mountains of New Guinea, probably mostly in unforested areas.

Notes. This genus is presumably derived from *Notagonum*. Its obvious adaptations (reduction of eyes, atrophy of wings in some species, and associated structural changes) are those which occur most often among ground-living mesophile Carabidae in temperate areas. The only species of *Gastragonum* which I have myself collected in any numbers (*terrestre*) was common under stones, and under strawberry plants in a missionary garden, in open country, not in forest, and always away from water. I found no other agonine in this situation. The several species of *Gastragonum*, perhaps excepting *laevisculptum*, apparently form a natural mesophile group which may be more or less confined to open areas of the mountains of New Guinea. This would account for the small number of specimens secured by Cheesman and Toxopeus, and so for the unfortunate number of uniques described below. These collectors apparently worked chiefly in forest (which, as experienced collectors well know, is the richest environment in New Guinea) or along brooks, and took many of their Carabidae with light traps, which would hardly catch at least the flightless species of *Gastragonum*.

Key to the Species of Gastragonum

1. Whole upper surface polished, without reticulate microsculpture; elytral striae strongly punctate (p. 224) . . . . *laevisculptum*
– Microsculpture present; elytral striae not punctate 2
2. Prothorax more broadly rounded, with sides relatively widely margined and not sinuate before base; (relatively weak frontal impressions distinguish this from all following species except *trechoides*) (p. 225) . . . *subrotundum*
– Prothorax less broadly rounded, often subcordate, with sides more narrowly margined and more or less sinuate before base 3
3. Sides of prothorax strongly sinuate before base; (frontal impressions rather deep, short-linear but not punctiform) 4
– Sides of prothorax weakly sinuate 5
4. Elytra not transversely impressed before middle; form a little broader; sides of prothorax more abruptly sinuate before base (p. 226) . . . . *terrestre*
– Elytra transversely impressed before middle; form a little more slender; sides of prothorax more broadly sinuate before base (p. 227) . . *terrestroides*
5. Elytra normal, subquadrate; frontal impressions very small, deep, punctiform (p. 227) . . . . *frontepunctum*
– Elytra oval; frontal impressions shallow, poorly defined (p. 228) . . *trechoides*

GASTRAGONUM LAEVISCULPTUM n. sp.

Description. With essential characters of genus as described above. Larger, broader, and less convex than usual (in genus); piceous-brown, appendages paler brown; upper surface polished, without detectable microsculpture (at 54×) but finely sparsely punctulate. *Head* .70 width prothorax; eyes small but abruptly prominent; genae about long as eyes, very oblique, convex in profile; front irregular, with moderate anterior impressions. *Prothorax* rather large; width/length 1.41; base/apex 1.26; anterior angles rather prominent, moderately rounded; sides weakly arcuate, vaguely subangulate at anterior-lateral setae, broadly but not strongly sinuate before nearly right, only slightly blunted posterior angles; lateral margins wide (in genus), moderately reflexed toward base; basal foveae moderate, irregular but scarcely punctate; disc normal; anterior and posterior marginal lines more or less entire but not deeply impressed. *Elytra* moderately wide, subparallel at middle, relatively convex compared with prothorax, not impressed; basal margin rounded and more than usually elevated at humeri; lateral margins rather wide (in genus); striae moderately impressed, rather strongly punctate; intervals convex. *Lower surface* impunctate except abdomen with some fine sparse punctation and inconspicuous pubescence. *Inner wings* vestigial; metepisterna shortened, not much more than ½ longer than wide. *Legs:* 4th hind-tarsal segment rather shallowly emarginate. *Male copulatory organs:* Fig. 54. *Measurements:* length 8.3; width about 3.4 mm.

Type. Holotype ♂ (Leiden Mus.) from Letterbox Camp, Snow Mts., **Neth. N. G.**, 3,600 m. (about 11,700 ft.), Sept. 1–12, 1938 (Toxopeus); unique.

Measured specimen. The type.

Notes. Although this interesting species has the technical characters of *Gastragonum*, I am not sure that it is really related to the other members of the genus. It may be independently derived, presumably from *Notagonum*. The characters which set this species apart from the others are general form, abruptly prominent "popped" eyes, absence of reticulate microsculpture, slight elevation of basal margin of elytra at humeri, punctation of elytral striae, pubescence of abdomen, and form of 4th hind-tarsal segment. I know of no species of any genus to which the present one is closely similar.

GASTRAGONUM SUBROTUNDUM n. sp.

Description. With characters of genus as described above. Form of convex *Stenolophus*; piceous, more or less iridescent (varying in different lights), appendages brown, lateral margins of prothorax moderately translucent-brown; microsculpture light and isodiametric on head, very light, fine and transverse on pronotum and elytra. *Head* .62 & .64 width prothorax; eyes small, moderately prominent; genae nearly as long as eyes, oblique, straight or slightly convex in profile; front strongly convex, frontal impressions slight; mentum tooth a little smaller than usual, triangular. *Prothorax* rounded-transverse; width/length 1.38 & 1.29; base/apex 1.30 & 1.33 (base measured at posterior-lateral setae); anterior angles only normally prominent, rather narrowly rounded; sides broadly arcuate through all or much of length, not sinuate posteriorly; posterior angles completely and broadly rounded out (♂ from Bismarck Range) or merely very obtuse (♀ from Snow Mts.); lateral margins moderate, wider basally, moderately reflexed; basal foveae rather small, scarcely punctate; disc normal; anterior and posterior marginal lines fine but entire. *Elytra* subquadrate, moderately elongate, rather strongly convex, slightly or scarcely impressed before middle; basal margin not or vaguely angulate at humeri; lateral margins rather narrow; striae moderately impressed, impunctate. *Lower surface* virtually impunctate; abdomen not pubescent. *Inner wings* fully developed in both specimens; metepisterna long. *Legs:* 4th hind-tarsal segment with rather short outer and still shorter inner lobe. *Male copulatory organs:* Fig. 55. *Measurements:* of ♂ from Bismarck Range, 6.6 by about 2.5; of ♀ from Snow Mts., 8.0 by about 3.0 mm.

Types. Holotype ♂ (M.C.Z. No. 28,665) from Chimbu Valley, Bismarck Range, **N-E. N. G.**, 5,000–7,500 ft., Oct. 1944 (Darlington), from an unrecorded habitat but not in forest; and 1 ♀ paratype from Ibele (Iebele) Camp, Snow Mts., **Neth. N. G.**, 2,250 m. (about 7,325 ft.), Nov. 1938 (Toxopeus).

Measured specimens. The types.

Notes. This species is sufficiently distinguished from others in the key to species of *Gastragonum*, above. The Snow Mts. specimen is larger than the type, with relatively narrower prothorax with evident, though very obtuse, posterior angles. If these differences prove to hold in series, they should be of at least subspecific value.

GASTRAGONUM TERRESTRE n. sp.

Description. With characters of genus as described above. Form (Fig. 9) of *Gastrellarius* (subgenus of *Pterostichus*); brownish-piceous, not distinctly iridescent, appendages yellowish-brown, lateral margins of prothorax moderately translucent-brown; microsculpture light and isodiametric on front (more distinct on occiput), very light and moderately transverse on disc of pronotum, more distinct (but still light) and moderately transverse on elytra. *Head* .65 & .64 width prothorax; eyes small but rather prominent; genae shorter than eyes, oblique; front strongly convex, with deep, short, linear frontal impressions extending onto clypeus; mentum tooth shorter than usual in *Notagonum*. *Prothorax* quadrate-subcordate; width/length 1.27 & 1.26; base/apex also 1.27 & 1.26; sides arcuate for much of length, strongly sinuate near base; basal angles approximately right, not blunted; lateral margins average (in genus); basal foveae moderate, poorly defined, more or less extensively punctate especially toward disc; disc normal; anterior and posterior marginal lines entire. *Elytra* subquadrate, of normal outline, rather strongly convex, not impressed on disc; basal margin not or slightly subangulate at humeri; lateral margins rather narrow; striae rather deeply impressed, irregular but not distinctly punctate. *Lower surface* sometimes with a few punctures at sides of mesosternum; abdomen not pubescent. *Inner wings* dimorphic, vestigial in 17 specimens (including type), fully developed in 2 specimens with same data; metepisterna rather long but a little variable, longest in the fully winged specimens. *Legs:* 4th hind-tarsal segment lobed but outer lobe short and inner one even a little shorter. *Male copu-*

latory organs as figured (Fig. 56). *Measurements:* length 6.2–6.9; width about 2.4–2.6 mm.

Types. Holotype ♂ (M.C.Z. No. 28,666) and 18 paratypes all from Chimbu Valley, Bismarck Range, **N-E. N. G.**, 5,000–7,500 ft., Oct. 1944 (Darlington).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This species is adequately compared with others in the key to species of *Gastragonum.* Its habitat is described in notes under the genus.

GASTRAGONUM TERRESTROIDES n. sp.

Description. Very close to *terrestre* and answering to the same description (see above) except in details given below. Larger and a little more elongate than *terrestre*; color same, but elytra faintly iridescent in some lights, with elytral microsculpture finer. *Head* .70 & .64 width prothorax. *Prothorax:* width/length 1.20 & 1.22 (narrower than in *terrestre*); base/apex 1.28 & 1.32; sides a little more broadly but still strongly sinuate before base. *Elytra* a little more elongate and with basal margin more distinctly angulate at humeri than in *terrestre,* and with disc distinctly impressed before middle in all (4) specimens. *Inner wings* fully developed in all specimens. Other characters as in *terrestre* (except male copulatory organs not compared). *Measurements:* length about 7.2–7.6; width slightly under 3.0 mm.

Types. Holotype ♂ (Leiden Mus.) and 1 broken ♂ paratype (M.C.Z. No. 28,667) from Ibele (Iebele) Camp, Snow Mts., **Neth. N. G.**, 2,250 m. (about 7,325 ft.), Nov.–Dec. 1938 (Toxopeus); 1 ♀ paratype from Moss Forest Camp, Snow Mts., 2,800 m. (about 9,100 ft.), Oct. 9–Nov. 5, 1938 (Toxopeus); and 1 ♀ paratype from Mt. Misim, Morobe Dist., **N-E. N. G.** (Stevens, M.C.Z.).

Measured specimens. The ♂ holotype and ♀ paratype from the Snow Mts.

Notes. This is so close to *terrestre* that, if it occurred only on the Snow Mts., I should probably consider it a subspecies, but its occurrence also on Mt. Misim has led me to treat *terrestroides* as a full species at least for the time being.

GASTRAGONUM FRONTEPUNCTUM n. sp.

Description. With characters of genus as described above. Similar to *terrestre* (of which see description, above) but differing in the following details. Similar to *terrestre* in form (except as noted below), color, and microsculpture. *Head* .65 width prothorax; eyes larger but less prominent than in *terrestre,* with genae short and oblique; frontal impressions very small but deep, round, punctiform, just behind clypeal suture. *Prothorax:* width/length 1.28; base/apex 1.20 (base relatively narrower than in *terrestre*); sides much less sinuate than in *terrestre*; basal angles obtuse, somewhat blunted. *Elytra, lower surface,* etc. about as in *terrestre. Inner wings* vestigial in single specimen, but metepisterna not much shortened. *Measurements:* length 6.7; width about 2.4 mm.

Type. Holotype ♀ (British Mus.) from Mt. Tafa, **Papua**, 8,500 ft., Feb. 1934 (Cheesman); unique. It is unfortunately somewhat crushed and broken, but the essential characters are not affected.

Measured specimen. The type.

Notes. The form of the frontal impressions is of course the outstanding character of this species.

GASTRAGONUM TRECHOIDES n. sp.

Description. With characters of genus as described above. Very small; form of a convex *Trechus*; color and microsculpture as in *terrestre* (see above). *Head* .65 width prothorax; eyes relatively larger than in *terrestre* but much less prominent; genae very short, oblique; frontal sulci slight. *Prothorax* rather small (in genus); width/length 1.24; base/apex 1.23; sides rather gently arcuate for most of length, slightly sinuate before base; basal angles obtuse, moderately rounded; lateral margins rather narrow, a little wider toward base, moderately reflexed; basal foveae moderate, not distinctly punctate; disc normal; anterior and posterior marginal lines entire. *Elytra* suboval, a little more narrowed in front than behind; basal margin obtusely but distinctly angulate at humeri; striae moderately impressed, not punctate; other details normal for genus. *Lower surface* virtually impunctate; abdomen not pubescent. *Inner wings* vestigial; metepisterna a little shortened. *Legs:* 4th hind-tarsal segment as in *terrestre. Measurements:* length 5.8; width 2.3 mm.

Type. Holotype ♀ (Leiden Mus.) from Baliem Camp, Snow Mts., **Neth. N. G.**, 1,700 m. (about 5,525 ft.), Nov. 16–27, 1938 (Toxopeus); unique.

Measured specimen. The type.

Notes. A distinct little species, sufficiently defined within the genus in the key to species of *Gastragonum.*

IDIAGONUM new genus

Diagnosis. Rather large (12.9–15.3 mm.), usually dull, black or brown, mountain-living forms, with wings vestigial, elytra with basal margin incomplete and with a partial extra (10th) interval, prosternal process setose, and wing-and-seta formula −w, ++, ++, − − −.

Description. Idiastes-like (Fig. 10); size and color as given above; microsculpture variable. *Head* large, more or less oval, with moderate or deep neck constriction; eyes very small but abruptly prominent, well separated from mouth below; both pairs supraocular setae present, anterior ones a little above anterior edges of eyes, posterior ones far behind and above eyes; antennae normal, with 3rd segment longer than 4th and 2 or more times long as 2nd; front very broadly, a little irregularly convex, slightly impressed each side anteriorly; mentum with a strong, triangular tooth, sometimes narrowly truncate at apex; ligula broad, bisetose; paraglossae slender, a little longer than ligula, free and bent inward toward apex; palpi slender, labial ones with 2nd segment bisetose. *Prothorax* more or less subcordate; anterior angles moderate or very prominent anteriorly; both pairs of lateral pronotal setae present, anterior ones at or a little before middle, posterior ones at basal angles. *Elytra* with basal margin absent inwardly, ending near bases of 4th striae, more or less angulate and prominent anteriorly at humeri; apices simple or nearly so; usual 9 intervals present and also a partial 10th one between 9th and margin posteriorly, outer intervals not much modified toward apex, 3rd without dorsal punctures; a slight longitudinal fold inside each elytron near outer edge, not reaching margin. *Inner wings* vestigial; metepisterna (without epimera a little longer than wide. *Lower surface* at most vaguely punctate; abdomen not pubescent; prosternal process with tip not margined but with conspicuous setae. *Legs* normally formed; hind tibiae not sulcate along outer edges; hind tarsi rather slender, lightly sulcate each side above; 4th hind-tarsal segment rather deeply emarginate but not or very briefly lobed; 5th hind-tarsal segment without obvious accessory setae; claws simple; sole of first 4 hind-tarsal segments rather densely setose each side below but with middle of sole narrowly bare. *Secondary sexual characters* normal except ♂ front tarsi less dilated than usual. *Male copulatory organs* as figured (Fig. 57).

Genotype. Idiagonum asperum n. sp. (below).

Generic distribution. At present known only from the Bismarck and Snow Mt. Ranges of New Guinea.

Notes. This new genus is superficially rather similar to *Idiastes* Andrewes of Mt. Kinabalu, Borneo, but it differs from *Idiastes* in the following notable characters: all normal supraocular and lateral pronotal setae present, basal margins of elytra incomplete, partial 10th elytral interval present, and prosternal process with setae. No one o these characters is necessarily very important, but together they suggest that *Idiagonum* is not directly related to *Idiastes* but has been independently derived perhaps from a *Colpodes*-like ancestor in the mountains of New Guinea. One of the alticoline *Colpodes* of New Guinea (*acuticauda*, described above) has some of the expected characteristics of such an ancestor. I should add that I have examined at the British Museum a dissected cotype of *Idiastes alaticollis* Andr. and that as a result I feel sure that *Idiastes* should go in the Agonini near *Colpodes*, not in the Pterostichini where Andrewes put it. The inner costa of the elytron does not reach the margin and is not really like that of a true pterostichine, and the male copulatory organs are agonine.

The partial extra (10th) elytral interval occurs in all specimens of all species of *Idiagonum*. A smaller or less well defined rudimentary 10th interval occurs also in some *Fortagonum* (below), but this is probably an example of parallelism rather than an indication of relationship.

Key to the Species of Idiagonum

1. Pronotum not transversely wrinkled (p. 230) . . . . *inasperum*
– Pronotal disc densely and extensively transversely wrinkled 2
2. Base of pronotum subequal to or narrower than apex, not distinctly margined (p. 231) . . . . *asperum*
– Base of pronotum slightly wider than apex, margined 3
3. Eyes, though small and abruptly prominent, forming only very obtuse angles with genae in profile from above; pronotum with many shallow transverse wrinkles, very finely longitudinally rugulose near both anterior and posterior margins; posterior marginal bead below level of surface of base of pronotum (p. 232) . . . . *muscorum*
– Eyes more abruptly prominent, forming conspicuous though still somewhat obtuse angles with genae; pronotum with fewer but deeper transverse wrinkles, more coarsely longitudinally rugulose near anterior margin but not distinctly rugulose near posterior margin; posterior marginal bead not below level of surface of base of pronotum (p. 232) . . . . *asperior*

IDIAGONUM INASPERUM n. sp.

Description. With characters of genus as described above, but more shining than usual, without transverse wrinkling of pronotum. Piceous-black or brownish-piceous (immature); moderately shining, not iridescent; upper surface finely and sparsely punctate and with reticulate microsculpture light and isodiametric on front of head, fine and transverse on pronotum, coarser and variable on elytra (♀) (nearly isodiametric on disc anteriorly, more transverse laterally and apically). *Head* .76 & .74 width prothorax; some transverse wrinkling behind and below eyes; mentum tooth truncate at apex. *Prothorax* rather large (in genus); width/length 1.28 & 1.25; base/apex 1.10 & 1.12; anterior angles moderately prominent; sides arcuate through much of length, not angulate at lateral setae, broadly sinuate before obtuse but nearly right and well formed basal angles; lateral margins moderately wide, reflexed; basal foveae poorly defined, shallow, impunctate, separated from margins by slight swellings (or they could be described as broad and deep, reaching margins, with bottoms slightly swollen); disc moderately convex; anterior and posterior marginal lines entire. *Elytra* slightly narrowed toward base, moderately convex; subapical sinuations absent or nearly so; apices simple, almost conjointly rounded, but sutural angles independently narrowly rounded; striae rather deep, impunctate; intervals moderately convex. *Measurements:* length 12.9–13.4; width 4.6–4.8 mm.

Types. Holotype ♀ (Leiden Mus.) and 1 ♀ paratype (M.C.Z. No. 28,668) both from Moss Forest Camp, Snow Mts., **Neth. N. G.**, 2,600–2,800 m. (about 8,450–9,100 ft.), Oct. 9–Nov. 5, 1938 (Toxopeus)

Measured specimens. The types.

Notes. This species is sufficiently distinguished from others in the key, above. The paratype has a few *longitudinal* wrinkles on head and pronotum which are, I think, due to warping of the surface. The specimen is slightly immature.

IDIAGONUM ASPERUM n. sp.

Description. With characters of genus as described above. Form as figured (Fig. 10). Rather dull black, legs and antennal bases piceous, outer segments of antennae brown; microsculpture of head fine but deeply impressed, isodiametric; that of pronotum fine, transverse; that of elytra apparently still finer and transverse but scarcely visible at 54×. *Head* .75 & .70 width prothorax; front with fine sparse punctulation as well as microreticulation and a little irregular wrinkling; much transverse wrinkling behind and below eyes; mentum tooth bluntly pointed. *Prothorax* subcordate; width/length 1.16 & 1.21; base/apex .98 & .98 (& .92); anterior angles moderately prominent; sides irregularly arcuate or nearly straight (and converging) anteriorly, angulate at anterior-lateral setae, then strongly converging posteriorly and strongly sinuate well before basal angles; latter right, accurately defined; lateral margins rather wide, reflexed; basal foveae deep, not punctate; disc strongly transversely rugulose, impunctate; apical and basal marginal areas longitudinally rugulose; anterior marginal line entire, posterior one vague or absent. *Elytra* distinctly narrowed toward base and rather strongly convex; subapical sinuations nearly absent; apices conjointly rounded except sutural angles slightly divergent and slightly produced (slightly variable); striae deep, not or slightly punctulate; intervals convex, with at most extremely fine, sparse, inconspicuous punctulation. *Male copulatory organs* as figured (Fig. 57). *Measurements:* length 13.8–15.3; width 4.7–5.2 mm.

Types. Holotype ♂ (M.C.Z. No. 28,669) and 12 paratypes all from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, 7,000–10,000 ft., Oct. 1944 (Darlington), taken under various cover on the ground in heavy forest.

Measured specimens. The ♂ holotype and 1 ♀ paratype (and in parentheses prothoracic base/apex ratio of another ♀).

Notes. Sufficiently compared with other species in the key above, and in the descriptions of the two following species.

IDIAGONUM MUSCORUM n. sp.

Description. With characters of genus as described above. Color and sculpture of *asperum* (of which see description, above) and form nearly similar, but broader, with elytra less narrowed anteriorly. *Head* .70 & .70 width prothorax, like that of *asperum* in all characters given. *Prothorax:* width/length 1.30 & 1.31; base/apex 1.08 & 1.10; anterior angles more prominent than in *asperum*; sides more evenly arcuate anteriorly, less angulate at anterior-lateral setae, and less strongly sinuate posteriorly, with posterior angles on the obtuse side of right; basal foveae and disc about as in *asperum*; posterior as well as anterior marginal line distinct, and posterior margin slightly below level of surface of base of pronotum. *Elytra* relatively broader (especially anteriorly) than in *asperum*; otherwise about same except sutural angles narrowly rounded or simply angulate, usually less prominent than in *asperum*. *Measurements:* length 13.4–15.2; width 4.9–5.4 mm.

Types. Holotype ♂ (Leiden Mus.) and 5 paratypes (2 in M.C.Z. No. 28,670) all from Moss Forest Camp, Snow Mts., **Neth. N. G.**, 2,600–2,800 m. (about 8,450–9,100 ft.), Oct. 9–Nov. 5, 1938 (Toxopeus)

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This is sufficiently compared with *asperum* above, and with other species in the key.

IDIAGONUM ASPERIOR n. sp.

Description. With characters of genus as described above. Color of the two preceding species (*asperum* and *muscorum*); form intermediate between the two. *Head* .72 & .74 width prothorax; eyes much more abruptly prominent than in the other species; sides of front irregularly flattened or depressed; neck-constriction deeper; mentum tooth bluntly pointed; sculpture of head about as in *asperum*. *Prothorax:* width/length 1.38 & 1.32; base/apex 1.09 & 1.07; anterior angles very prominent, making prothorax appear longer than measurements above suggest; sides angulate at anterior setae, rather broadly, moderately sinuate before basal angles; latter slightly obtuse or nearly right, very well defined; basal foveae deep and simple, as in *asperum*; disc with fewer but deeper transverse wrinkles than in *asperum* or *muscorum* and with some fine sparse punctulation, coarsely longitudinally rugulose near apex, irregular but not distinctly rugulose near base; posterior as well as anterior marginal line distinct, posterior margin on same level as surface of base of pronotum. *Elytra* with apices simple, broadly conjointly rounded (as in other species) and with sutural angles narrowly rounded; striae and intervals about as in preceding species but intervals a little more plainly though still finely and sparsely punctulate. *Measurements:* length 13.1–13.8; width 4.9–5.3 mm.

Types. Holotype ♂ (Leiden Mus.) and 4 paratypes (2 in M.C.Z. No. 28,671) from Moss Forest Camp, Snow Mts., **Neth. N. G.**, 2,600–2,800 m. (about 8,450–9,100 ft.), Oct. 9–Nov. 5, 1938; and 1 paratype from Top Camp, Snow Mts., 2,100 m. (about 6,825 ft.), Jan. 29, 1939 (all collected by Toxopeus).

Measured specimens. The ♂ holotype and 1 ♀ paratype from Moss Forest Camp.

Notes. It is surprising to find a second rugulose species of this genus with exactly the same data as *muscorum*. Possibly the two occur in different forest tracts, or are otherwise separated. It is conceivable that the two are forms of one dimorphic species, but this seems to me unlikely. Each is represented by several specimens and each is uniformly characterized by several seemingly independent structural details.

MONTAGONUM new genus

Diagnosis. Based on one species, so generic and specific characters not separable, but genus characterized by convex *Calathus*-like form, atrophied wings, wing-and-seta formula −w, ++, −+, +++ (but single punctures of 3rd elytral interval sometimes missing) with posterior-lateral pronotal setae on flat surface of margins well before basal angles, absence of obvious accessory setae on 5th hind-tarsal segment, etc.

Description. See that of single species, below.

Genotype. *Montagonum toxopeanum* n. sp., below.

Generic distribution. At present known only from one locality at a high altitude (at or slightly above timber line) on the Snow Mountains of Netherlands New Guinea.

Notes. In atrophied wings and to some extent in appearance this new genus resembles certain *Nebriagonum* (below), but this is probably a result of similar adaptation to a similar habitat rather than an indication of relationship. The pattern of standard setae is different from any *Nebriagonum.* The position of the posterior-lateral pronotal setae, on the flat surface of the margins, is somewhat like the position of these setae in certain *Altagonum* (*latilimbus, paralimbus, scapha*), although in the latter the setae are not so far forward. I suspect that *Montagonum* has been derived independently from an *Altagonum* by atrophy of wings and other appropriate changes.

MONTAGONUM TOXOPEANUM n. sp.

Description. Convex *Calathus*-like (Fig. 11); piceous-black, appendages dark-reddish, lateral margins of prothorax and elytra faintly if at all translucent; upper surface impunctate, moderately shining, not iridescent; microsculpture normal, very distinct. *Head* rather small, .57 & .57 width prothorax; eyes reduced in size but more prominent than usual; genae about as long as eyes, oblique; both pairs of supraocular setae present, posterior ones well behind line of posterior edges of eyes; antennae rather short, normal in structure; neck not impressed above; front irregularly convex, with slight frontal impressions; mentum tooth triangular. *Prothorax* rather long, widest near middle, rather strongly narrowed in front, moderately so behind; width/length 1.13 & 1.11; base/apex 1.41 & 1.50; anterior angles moderately advanced, rounded-acute; sides weakly arcuate for much of length, more or less straight (and converging) or even faintly sinuate toward base; basal angles a little obtuse and rather narrowly rounded; lateral margins very narrow anteriorly, broader but very poorly defined posteriorly; anterior-lateral setae absent, posterior-lateral ones on flat margins just inside of thickened marginal beads about 1/6 of prothoracic length before apparent basal angles; basal foveae very shallow and poorly defined, sometimes with a slight swelling at middle, not punctate; disc convex, with light median line, and with transverse impressions scarcely indicated; anterior marginal line entire, posterior one faint or broadly interrupted at middle. *Elytra* with sides more rounded and disc more convex than usual in tribe; disc not impressed; anterior margin entire, about rectangular at humeri; lateral margins moderate; subapical sinuations absent, sides curving smoothly almost to suture, so apices almost conjointly rounded; sutural angles narrowly rounded, slightly dehiscent but not produced, not denticulate; striae moderately impressed, not punctate; intervals slightly convex, 8th and 9th not much modified toward apex, 3rd normally 3-punctate except punctures somewhat variable in anterior-posterior spacing, and single punctures sometimes missing (left anterior puncture missing in type, right posterior one missing in 2nd measured specimen). *Inner wings* vestigial; metepisterna slightly shortened. *Lower surface* impunctate; abdomen not pubescent; prosternal process simple. *Legs:* 4th hind-tarsal segment simply emarginate; 5th hind-tarsal segment with apparent vestigial but usually not obvious accessory setae (type has 1 obvious seta on outer-lower edge of right 5th hind-tarsal segment about middle of its length). *Secondary sexual characters* normal. *Male copulatory organs* as figured (Fig. 58). *Measurements:* length 8.7–9.3; width 3.2–3.5 mm.

Types. Holotype ♂ (Leiden Mus.) and 5 paratypes (2 in M.C.Z. No. 28,672) all from Letterbox Camp, Snow Mts., **Neth. N. G.**, 3,600 m. (about 11,700 ft.), Sept. 1–12, 1938 (Toxopeus).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. The possible relationships of this species are discussed under the genus.

I take great pleasure in naming this distinct and interesting high-altitude form for Mr. L. J. Toxopeus, who obtained the types and so many other fine Carabidae on the Snow Mts. of New Guinea. I have used the name *toxopeanum* rather than *toxopei* because the latter has been employed by Andrewes for a species of *Colpodes* from Buru.

NEBRIAGONUM new genus

Diagnosis. Within the New Guinean agonine complex this genus is most simply characterized by atrophied wings plus *either* a very large head (.90 or more width prothorax) *or* presence of obvious accessory setae on the 5th hind-tarsal segment. Additional noteworthy generic characters are eyes small; head with distinct but variable neck-constriction; prothorax small or moderate in size and usually rather elongate; elytra more or less oval, with dorsal punctures irregular or absent. The wing-and-seta formula is confusingly variable: −w, (+)+, (−) (−), (−) (−) (−). Some of the species have rather the appearance of large-headed, convex species of *Nebria* with oval elytra. The size-range is from 7.7 to 14.3 mm.

Description. Form variable; black or brownish with appendages not much paler; upper surface only moderately shining, not or (*transitior*) faintly metallic, not iridescent; upper surface including pronotal foveae virtually impunctate; microsculpture always distinct, about isodiametric on head, more or less transverse (sometimes only slightly so) on pronotum and elytra. *Head* moderate to very large; eyes rather small, variable in form; both pairs supraocular setae present except anterior pair usually absent in *percephalum*; posterior pair slightly or much behind line of posterior edges of eyes; neck-constriction always present, but variable, sometimes only slightly impressed above; anterior frontal impressions moderate, irregular; front often impressed also between eyes, the impressions often being 4 in number and forming a rectangle narrowest anteriorly; antennae normal, varying in length; mentum tooth triangular with apex variable (pointed, blunted, or slightly emarginate). *Prothorax* rather narrow but variable in form; lateral pronotal setae present only in *cephalum*, absent in other species; basal foveae moderate or small, not sharply defined; disc more or less strongly convex, with usual middle line and transverse impressions more or less lightly impressed; anterior marginal line entire, posterior one also usually entire but less impressed. *Elytra* more or less oval, usually strongly convex; basal margin entire, differently subangulate or angulate at humeri in different species; subapical sinuations absent or nearly so; apices usually simply and more or less independently rounded, rarely (*arboreum*) each with a very short spine; striae deeply to very lightly impressed in different species, not or (*arboreum*) faintly punctulate; 8th and 9th intervals not much modified toward apex; 3rd interval with or without (irregular) dorsal punctures. *Lower surface* impunctate or nearly so; abdomen not pubescent; prosternal process simple. *Inner wings* vestigial; metepisterna more or less shortened. *Legs* normally formed; hind tibiae not sulcate along outer edges; hind tarsi slender, not or only slightly sulcate at sides above; 4th hind-tarsal segment simply emarginate in *subcephalum*, lobed in other species, with outer lobe longer than inner; 5th hind-tarsal segment with or without obvious accessory setae in different species. *Secondary sexual characters* normal. *Male copulatory organs* as figured (Figs. 59 & 60).

Genotype. Nebriagonum cephalum n. sp. (below).

Generic distribution. At present known only from 5 species from the Bismarck Range and 1 from the Snow Mountains, New Guinea.

Notes. Although there is extraordinary variation in some characters in this new genus, I am convinced that it is a natural one, except perhaps for *N. subcephalum* which is somewhat isolated in structure (see notes under its description) as well as geographically. The 5 species from the Bismarck Range form a remarkable and nearly continuous series. *N. cephalum* has all normal supraocular and lateral pronotal setae except that one or both posterior-lateral pronotal setae are missing in a few individuals; it has some (irregular) dorsal punctures on the 3rd elytral intervals; and the 5th hind-tarsal segment lacks obvious accessory setae. *N. percephalum* is superficially very similar, differing only slightly in details of form, depth of elytral striae, etc., but has lost the anterior supraocular setae (except that the anterior one is present on one side in one individual), both pairs of pronotal setae, and all dorsal punctures of the 3rd elytral intervals; (the 5th hind-tarsal segment is without obvious accessory setae, as in *cephalum*). *N. transitum* too is not very different from *cephalum* superficially (the prothorax is more rounded but still with narrow margins, the elytra are less deeply striate, etc.), but it has lost both pairs of lateral pronotal setae and most of the dorsal punctures of the 3rd elytral intervals (it has both pairs of supraoculars), and it has a few (usually 2 or 3 on each side) small but distinct accessory setae on the 5th hind-tarsal segment. *N. transitior* in turn is not very different from *transitum*, with elytral apices still simple, but it has wider prothoracic margins and better developed accessory setae on the 5th hind-tarsal segment, and it has completely lost all dorsal punctures of the 3rd elytral intervals. Finally, *arboreum* is not very different from *transitior*, but is larger, with short-spined elytral apices, and different in other details, including retention of at least the posterior puncture of the 3rd elytral interval. These 5 species form an interesting sequence in habits, too. *N. cephalum* and *percephalum* are hydrophiles which occur primarily by rapid mountain brooks in and above the highest forest on Mt. Wilhelm, and *cephalum* occurs also in seepage areas up to about 14,000 ft., the highest altitude at which I found any Carabidae on the mountain. *N. transitum* is a mesophile which is common on the ground under cover away from water, chiefly in open, grassy country above timber line. *N. transitior* is another ground-living mesophile, but my 6 specimens of it were all found in forest. And *N. arboreum* is apparently arboreal; both my specimens of it were found above the ground, one in the thatch of an old shelter. I do not mean to imply that these 5 species form a simple linear series. Their relationships are probably complex. But I do feel sure that they represent one stock which has radiated on the Bismarck Range, or at least in a limited area in the mountains of New Guinea. These species are now isolated from each other at least partly by ecological factors, but it would be unwise to assume that they have evolved in their present positions as a result of ecological isolation. They are very distinct species and they may have had complex histories (*cf.* "Role of geographical isolation" in the introduction, above).

Key to the Species of Nebriagonum

1. Fourth hind-tarsal segment emarginate, not lobed; (see also notes under species) (Snow Mts.) (p. 238) . . . . *subcephalum*

– Fourth hind-tarsal segment lobed, outer lobe longer than inner (Bismarck Range 2

2. Head very large, about .90 or more width prothorax; 5th hind-tarsal segment without obvious accessory setae 3

– Head relatively narrower; 5th hind-tarsal segment with obvious accessory setae 4

3. Both pairs (or sometimes only anterior pair) of lateral pronotal setae, both pairs of supraocular setae, and some punctures of 3rd elytral intervals present (p. 239) . . . . *cephalum*

– Both pairs of lateral prothoracic setae, anterior supraoculars (usually), and all punctures of 3rd elytral intervals absent (p. 240) . . . . *percephalum*

4. Prothorax narrowly margined; length 8.4–10.3 mm. (p. 241) . . . . *transitum*

– Prothorax more widely margined; size larger 5

5. Elytral apices simple; length 11.3–11.9 mm. (p. 241) . . . . *transitior*

– Elytral apices each with a short spine; length 12.9–14.3 mm. (p. 242) . . . . . *arboreum*

NEBRIAGONUM SUBCEPHALUM n. sp.

Description. With main characters of genus as described above, but exceptional in several details. Form more normally agonine than in other *Nebriagonum*, with head narrower, prothorax less modified, and elytra less oval. *Head* .73 & .76 width prothorax; eyes small, only moderately prominent; genae about as long as eyes, slightly convex in profile; both pairs supraocular setae present; neck constriction vague, shallow; front only slightly impressed behind usual anterior impressions. *Prothorax* of moderate size, only moderately elongate; width/length 1.09 & 1.08; base/apex 1.18 & 1.21; anterior angles only slightly prominent; sides broadly, not strongly arcuate, then slightly or moderately sinuate before well formed, nearly right, only slightly blunted posterior angles; lateral margins rather narrow, without setae. *Elytra* with basal margin distinctly but obtusely angulate at humeri; apices simple, nearly as in *cephalum* (below); striae moderately impressed; 3rd interval impunctate. *Legs:* 4th hind-tarsal segment simply emarginate, not lobed; 5th hind-tarsal segment with obvious accessory setae. *Measurements:* length 9.8–10.0; width 3.6–3.8 mm.

Types. Holotype ♂ (Leiden Mus.) and 3 paratypes (1 in M.C.Z. No. 28,673) all from Lake Habbema, Snow Mts., **Neth. N. G.**, 3,300 m. (about 10,725 ft.), Oct. 2, 1938 (Toxopeus).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This species is exceptional in *Nebriagonum* in that the head is only moderately large, with vague neck-constriction; the posterior angles of the prothorax accurately formed; and the 4th hind-tarsal segment only emarginate, not lobed. However, the species is not too different from some more typical *Nebriagonum* in form; the arrangement of fixed setae (both pairs of supraoculars present, both pairs of lateral pronotals absent, and all punctures of 3rd elytral intervals absent) is the same as in some *Nebriagonum*; it has obvious accessory setae on the 5th hind-tarsal segment as do some *Nebriagonum*; and it probably occupies a habitat like that of *Nebriagonum*, occurring on the open grassy slopes or in the highest forest fringes above Lake Habbema in the Snow Mountains much as *Nebriagonum transitum* occurs on the slopes above Lakes Aunde and Piunde on Mt. Wilhelm. I think that *subcephalum* probably is genetically a *Nebriagonum* but that it is less closely related to any of the species of the Bismarck Range than the latter are to each other.

NEBRIAGONUM CEPHALUM n. sp.

Description. With characters of genus as described above. Form as figured (Fig. 12). *Head* appearing wider than prothorax but actually a little narrower, .96 & .90 as wide in measured specimens; eyes small, only moderately prominent; both pairs of supraocular setae present; genae as long or longer than eyes, convex in profile; neck-constriction rather deep; front usually with irregular impressions behind normal anterior ones. *Prothorax* small, appearing longer than wide but by measurement slightly wider; width/length 1.09 & 1.07, with greatest width about ⅓ behind apex; base/apex 1.03 & 1.02 if base measured across posterior setae, but base narrower if measured at apparent posterior angles; anterior angles hardly at all produced; sides irregularly, rather weakly arcuate, usually slightly sinuate before and subangulate at posterior-lateral setae, and then extended backward and slightly or strongly inward to narrowly rounded apparent posterior angles; lateral margins narrow, each with usual 2 setae in most cases, but posterior setae missing (not broken off) on one or both sides in several individuals. *Elytra* with basal margin distinctly but very obtusely angulate at humeri; apices irregularly broadly rounded to near sutural angles; latter narrowly rounded; striae moderately impressed; each 3rd interval with usually 3 or 4 (sometimes only 2) dorsal punctures irregularly placed as to both length and width of interval, and often very differently arranged on opposite elytra of one individual. *Legs:* 4th hind-tarsal segment lobed; 5th hind-tarsal segment without obvious accessory setae. *Male copulatory organs* as figured (Fig. 59). *Measurements:* length 7.7–9.4; width 2.8–3.3 mm.

Types. Holotype ♂ (M.C.Z. No. 28,674) and 62 paratypes all from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, Oct. 1944 (Darlington). The type and 21 paratypes are from above the forest line (above 10,000 ft.) and 5 additional paratypes are from still higher, about

14,000 ft., not far below the rocky summit of the mountain, which I suppose to be 15,400 ft. high. The remaining 36 paratypes are from the forest zone between 7,000 & 10,000 ft. Actually all the specimens were taken along the Chim River or its highest tributaries, beside the running water, in and above the forest zone, or in seepage areas at still higher altitudes.

Measured specimens. The ♂ holotype and 1 ♀ paratype with same data.

Notes. Both the structure and habits of this species have been compared with those of other members of the genus in the generic discussion, above.

NEBRIAGONUM PERCEPHALUM n. sp.

Description. With characters of genus as described above. Larger and a little more slender than the preceding (*cephalum*). *Head* appearing wider than prothorax, but actually only .95 & .93 as wide; eyes small, more abruptly prominent than in *cephalum*; posterior supraocular setae present, anterior ones absent except present on right side in one individual; genae longer than eyes, strongly convex in profile; neck-constriction strongly marked; front conspicuously impressed between eyes, the impressed area divided into about 4 poorly defined, more or less longitudinal parts. *Prothorax* elongate, appearing much longer than wide but actually about as long; width/length .99 & 1.04; base/apex 1.03 & 1.08; anterior angles a little prominent anteriorly; sides very broadly and slightly arcuate, more or less strongly sinuate before nearly right but slightly blunted or very narrowly rounded posterior angles; lateral margins narrow, without setae. *Elytra* with basal margin strongly (obtusely to almost rectangularly) angulate at humeri; apices simple, as in *cephalum*; striae deeply impressed at least at sides of elytra; 3rd intervals impunctate. *Legs:* 4th hind-tarsal segment lobed; 5th hind-tarsal segment without obvious accessory setae. *Measurements:* length 9.3–10.5; width 3.1–3.6 mm.

Types. Holotype ♂ (M.C.Z. No. 28,675) and 11 paratypes all from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, Oct. 1944 (Darlington). The type and 10 paratypes are from the forest zone between 7,000 & 10,000 ft.; 1 paratype, from above the forest (above 10,000 ft.). Actually all were taken on the banks of the Chim River or its tributaries, in company with *cephalum*.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This species is sufficiently discussed and compared under the genus and in the key to species of *Nebriagonum*.

NEBRIAGONUM TRANSITUM n. sp.

Description. With characters of genus as described above. Slightly stouter than any of the preceding species, very convex, almost like a stout *Broscus* in appearance. *Head* .82 & .82 width prothorax; eyes small, rather abruptly prominent; genae longer than eyes, convex in profile; both pairs supraocular setae present; neck-constriction well marked, moderately impressed above; front rather lightly impressed (4 poorly defined impressions) between eyes. *Prothorax* of moderate size; width/length 1.12 & 1.13; base about wide as apex (angles too rounded to measure base exactly); anterior angles slightly advanced; sides more arcuate and much more converging posteriorly than in *cephalum*, straight or slightly sinuate before obtuse, rather narrowly rounded basal angles; lateral margins narrow, without setae. *Elytra* with basal margin vaguely or distinctly (but very obtusely) angulate at humeri; apices simple, about as in *cephalum*; striae lightly impressed; dorsal punctures of 3rd elytral intervals variable, rarely entirely absent, anterior puncture usually present on one or both elytra and posterior one often present on one or both elytra too, but middle puncture rarely if ever present. *Legs:* 4th hind-tarsal segment lobed; 5th hind-tarsal segment usually with small but distinct accessory setae (usually about 2 each side of segment, but in some cases they are broken off or possibly absent). *Measurements:* length 8.4–10.3; width 3.1–3.7 mm.

Types. Holotype ♂ (M.C.Z. No. 28,676) and 48 paratypes all from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, Oct. 1944 (Darlington); the type and 36 paratypes are from open grassy slopes above 10,000 ft.; the remaining 12 paratypes, from forest between 7,000 & 10,000 ft. (presumably from the upper forest fringes).

Measured specimens. The ♂ holotype and 1 ♀ paratype with the same data.

Notes. This species is discussed under the genus and defined in the key to species of *Nebriagonum.*

NEBRIAGONUM TRANSITIOR n. sp.

Description. With characters of genus as described above. Larger and more slender than the preceding (*transitum*), with a faint purple tinge on elytra not present in other species of genus. *Head* .84 & .83 width prothorax; eyes small, rather abruptly prominent; genae longer than eyes, convex in profile; both pairs supraocular setae present; neck-constriction moderately impressed above; front with 4 slight impressions between eyes. *Prothorax* long; width/length .98 & 1.01; base about wide as apex; anterior angles scarcely at all prominent;

sides rather weakly arcuate for much of length, rather strongly converging and straight or slightly sinuate posteriorly; posterior angles obtuse, rather narrowly rounded; lateral margins moderate (wider than in preceding forms) but scarcely wider posteriorly than anteriorly and not much reflexed, without setae. *Elytra* with basal margin moderately though somewhat obtusely angulate at humeri; apices simple, about as in *cephalum*; striae rather lightly impressed; 3rd intervals impunctate in all specimens. *Legs:* 4th hind-tarsal segment lobed; 5th hind-tarsal segment with several obvious accessory setae each side. *Male copulatory organs:* Fig. 60. *Measurements:* length 11.3–11.9; width 3.7–4.0 mm.

Types. Holotype ♂ (M.C.Z. No. 28,677) and 5 paratypes all from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, 7,000–10,000 ft. (in forest), Oct. 1944 (Darlington).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This species too has been discussed and compared under the genus and in the key to species of *Nebriagonum.*

NEBRIAGONUM ARBOREUM n. sp.

Description. With characters of genus as described above. Still larger than preceding (*transitior*), with elytra less convex, more elongate, and more narrowed toward humeri. *Head* .79 & .78 width prothorax; eyes rather small, not abruptly prominent, almost continuing lines of genae; latter long as or slightly longer than eyes, slightly convex in profile; both pairs supraocular setae present; neck-constriction distinct but not much impressed above; front scarcely impressed between eyes behind usual anterior impressions. *Prothorax* long; width/length .99 & 1.06; base appearing slightly narrower than apex, but posterior angles too rounded for accurate measurement of base; anterior angles slightly advanced; sides broadly arcuate anteriorly, strongly converging from about anterior ⅓ toward base, slightly sinuate before broadly rounded posterior angles; lateral margins rather wide (wider than in *transitior*) but scarcely wider posteriorly than anteriorly, moderately reflexed, without setae; base broadly, slightly arcuate or lobed, the lobe smoothly rounded into posterior angles. *Elytra* rather long and slender, much narrowed anteriorly, less convex than usual in genus; basal margin strongly but not quite rectangularly angulate at humeri; apices each with a very short, stout spine about opposite 3rd or 4th interval, base of spine running sinuously but smoothly into both lateral and sutural margins of elytron, without other angulation; striae very lightly impressed, irregular or faintly punctulate; 3rd interval of ♂ type with only posterior puncture present, near top of declivity on each elytron, of ♀ paratype with only posterior puncture on left elytron but middle and posterior ones on right elytron. *Legs:* 4th hind-tarsal segment lobed; 5th hind-tarsal segment with a row of conspicuous accessory setae each side. *Measurements:* length (♂ ♀) 12.9–14.3; width 4.2–4.8 mm.

Types. Holotype ♂ (M.C.Z. No. 28,678) and 1 ♀ paratype both from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, 7,000–10,000 ft. (forest), Oct. 1944 (Darlington).

Measured specimens. The types.

Notes. See again the generic discussion and the key to species of *Nebriagonum*. The copulatory organs of the ♂ type are too unformed to draw.

LAEVAGONUM new genus

Diagnosis. Small (5.5–8.4 mm.), *Europhilus-* or *Calathus-* or cistelid-like; prothorax and elytra with outlines smoothly but more or less independently rounded and with discs smoothly convex; basolateral foveae of pronotum obsolete; wing-and-seta formula −w, ++, (−)−, − − −.

Description. Form as indicated above; brown or piceous, with appendages brownish or yellowish; surface moderately shining, not iridescent, nearly impunctate above except elytral intervals often vaguely punctulate; microsculpture normal except only slightly transverse on elytra, usually less so than on pronotum. *Head* small, more or less elongate; eyes more or less reduced in size and only slightly prominent; both pairs supraocular setae present, posterior ones slightly or distinctly behind line of posterior edges of eyes; antennae normal; neck slightly or not impressed above; front convex, with small anterior impressions; mentum tooth triangular with apex more or less blunted. *Prothorax* with sides smoothly rounded for whole length, or sometimes straighter (and of course more or less converging) toward base; lateral margins very narrow, usually without setae but anterior-lateral ones present in *subcitum*; anterior angles more or less distinct, obtuse or narrowly rounded, not produced beyond curve of broadly emarginate anterior edge of prothorax; posterior angles moderately or broadly rounded; disc with usual median line (sometimes very light) but transverse impressions slight or absent; anterior marginal line usually entire but often faint and sometimes interrupted at middle, posterior one faint or widely interrupted or obsolete. *Elytra* with basal margin entire or nearly so, rectangular or nearly so at humeri except only obtusely angulate in *subcitum*; lateral margins more or less narrow; sides forming nearly smooth curves from humeri to apices; subapical sinuations obsolete or nearly so; apices narrowly, more or less independently rounded, rarely with sutural angles denticulate (*citum* only); striae rather lightly impressed, not distinctly punctate but often irregular or vaguely punctulate; intervals slightly convex, outer ones not much modified toward apex, 3rd impunctate. *Inner wings* vestigial. *Lower surface* impunctate or nearly so; abdomen not pubescent; prosternal process simple. *Legs:* hind tibiae not sulcate along outer edges; 4th hind-tarsal segment emarginate, not lobed; 5th hind-tarsal segment without obvious accessory setae; claws simple. *Secondary sexual characters* normal. *Male copulatory organs* as figured (Figs. 61–63).

Genotype. *Laevagonum cistelum* n. sp. (below).

Generic distribution. Known only from high altitudes on the Bismarck Range, N-E. N. G.

Notes. The presence of anterior-lateral pronotal setae in one species argues against a derivation of this genus from *Altagonum.* It has perhaps been derived independently from *Notagonum* or from a *Gastragonum*-like ancestor. The species of *Laevagonum,* which are perfectly distinct but obviously rather closely related to each other, constitute another good example (*cf. Nebriagonum*) of apparent speciation in a limited mountainous area. All the species were found in or just above one continuous piece of heavy mountain forest. I have no record of the habitat of *subcitum,* the most distinct of the four, except that it occurred in forest. Of the other three species, *citum,* with the smallest eyes, was found under comparatively deep stones and logs in forest and may be incipiently subterranean; *cistelum,* under various cover on the ground in forest; and *subcistelum,* under cover on the ground in open grassy areas just above the upper edges of the forest. The fact that these species are all flightless is consistent with their apparent isolation in slightly separated habitats. However, it does not necessarily follow that they originated as a result of ecological isolation, as I have already noted in the introduction.

All the species of this genus share many characters covered in the preceding generic description, so their individual descriptions can be brief.

Key to the Species of Laevagonum

1. Anterior-lateral pronotal setae present; elytral margin very obtusely angulate at humeri; (*Europhilus*-like) (p. 245) . . . . *subcitum*
– Anterior-lateral (as well as posterior-lateral) pronotal setae absent; elytral margin rectangular or nearly so at humeri 2
2. *Europhilus*-like; slender, prothorax more elongate, width/length .98 & .99; sutural angles of elytra denticulate (p. 245) . . . . *citum*
– Cistelid- or *Calathus*-like; prothorax shorter, width/length 1.15 to 1.39; sutural angles of elytra not denticulate 3

3. Larger (7.0–8.4 mm.); browner; elytra relatively longer and less rounded (p. 246) . . . . *cistelum*
– Smaller (5.5–6.4 mm.); blacker; elytra relatively shorter and more rounded (p. 246) . . . . *subcistelum*

LAEVAGONUM SUBCITUM n. sp.

Description. With characters of genus as described above. *Europhilus*-like. *Head* only moderately elongate, .69 & .65 width prothorax; eyes slightly longer than and somewhat more prominent than genae. *Prothorax* subquadrate but with moderately rounded sides; width/length 1.07 & 1.15; base slightly or scarcely wider than apex (angles too rounded for exact measurement of base); anterior-lateral seta (or puncture marking its position) present slightly before middle of prothoracic length on both sides in both specimens. *Elytra* with basal margin only very obtusely angulate at humeri; lateral margins only moderately narrow; apices with sutural angles obtuse, poorly defined, not denticulate. *Male copulatory organs:* Fig. 61. *Measurements:* length 6.3–6.4; width about 2.2 mm.

Types. Holotype ♂ (M.C.Z. No. 28,679) and 1 ♀ paratype both from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, 7,000–10,000 ft. (forest), Oct. 1944 (Darlington).

Measured specimens. The types.

Notes. Sufficiently compared with other species in key above.

LAEVAGONUM CITUM n. sp.

Description. With characters of genus as described above. *Europhilus*-like, elongate. *Head* relatively elongate, .63 & .62 width prothorax; eyes as long as or slightly longer than and scarcely or slightly more prominent than genae. *Prothorax* elongate, appearing longer than wide and by measurement very slightly so; width/length .98 & .99; base slightly wider than apex (angles too rounded for exact measurement of base). *Elytra* with basal margin about rectangular at humeri; lateral margins rather narrow; sutural angles usually conspicuously denticulate, but only vaguely so in 1 paratype. *Male copulatory organs:* Fig. 62. *Measurements:* length 7.2–8.4; width 2.4–2.8 mm.

Types. Holotype ♂ (M.C.Z. No. 28,680) and 3 (♀ ♀) paratypes all from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, 7,000–10,000 ft. (forest), Oct. 1944 (Darlington).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This species is distinguished from others in the key above, and its habits are indicated in discussion under the genus.

LAEVAGONUM CISTELUM n. sp.

Description. With characters of genus as described above. Rather slender *Calathus*- or (even more) cistelid-like (Fig. 13). *Head* small and not very elongate, .53 & .51 width prothorax; eyes longer than genae but scarcely or only slightly more prominent. *Prothorax* strongly narrowed in front, much less so behind; width/length 1.24 & 1.39; base/apex about 1.8 & 1.7 (angles too rounded for exact measurement of base); sides variably, weakly to rather strongly rounded; basal angles also rather variable, moderately to very broadly rounded. *Elytra* with basal margin about rectangular at humeri; lateral margins narrow; apices with sutural angles narrowly rounded or somewhat distinct, but not denticulate. *Male copulatory organs* as figured (Fig. 63). *Measurements:* length 7.0–8.4; width 2.4–2.9 mm.

Types. Holotype ♂ (M.C.Z. No. 28,681) and 9 paratypes all from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, 7,000–10,000 ft. (forest), Oct. 1944 (Darlington).

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This too is sufficiently compared with other species in the key above, and its habitat is indicated in notes under the genus.

LAEVAGONUM SUBCISTELUM n. sp.

Description. With characters of genus as described above. *Calathus*-like. *Head* small, only moderately elongate, .60 & .62 width prothorax; eyes longer than and a little more prominent than genae. *Prothorax* a little longer and less narrowed in front than in *cistelum*; width/length 1.20 & 1.15; base/apex 1.4, more or less (angles too rounded for exact measurement of base); sides moderately rounded throughout or straighter toward base; basal angles rather broadly rounded. *Elytra* relatively shorter and more rounded than in *cistelum*; basal margin strongly but usually somewhat obtusely angulate at humeri; lateral margins narrow; apices with sutural angles narrowly rounded, or at most faint and obtuse, not denticulate. *Measurements:* length 5.5–6.4; width 2.0–2.3 mm.

Types. Holotype ♂ (M.C.Z. No. 28,682) and 7 paratypes all from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, slightly above 10,000 ft., Oct. 1944 (Darlington), under cover in open grassy places a little above the forest line.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. Adequately compared in key above, and mentioned also in discussion under the genus.

FORTAGONUM new genus

Diagnosis. Moderate-sized (8.8–12.4 mm.), heavily built, broadly subparallel or fusiform, more or less strongly convex; inner wings vestigial; wing-and-seta formula −w, −(+), − −, (−) (−) (−) (note anterior supraoculars absent).

Description. Form as indicated above; black or brownish-black, elytra sometimes more or less iridescent or purplish; lateral margins of prothorax and elytra not distinctly translucent; appendages piceous or reddish; upper surface moderately shining; microsculpture more or less normal, but differing in detail in different species. *Head* variable; mandibles sometimes (not always) strikingly long, slender, and nearly straight; eyes more or less reduced but very variable in prominence; anterior supraocular setae absent, posterior ones present except absent in *bufo*, slightly behind or almost between posterior edges of eyes; antennae normal; neck not impressed above; front variable; mentum tooth triangular, sometimes more or less blunted or subtruncate at tip. *Prothorax* with anterior angles broadly and strongly advanced, with apices right-acute except as blunted or narrowly rounded; lateral margins wide at least basally but sometimes not sharply differentiated from disc; lateral pronotal setae absent; basal foveae obsolete or nearly so, scarcely distinct from wide basal parts of margins; base more or less normal; anterior marginal line entire, posterior one faint or obsolete. *Elytra* always broad at base and usually rather short, not impressed on disc; variable in many details but always more or less narrowly margined at sides, with apices not armed; striae moderately to rather deeply impressed, impunctate; a more or less distinct partial 10th interval often (not always) present posteriorly. *Inner wings* vestigial. *Lower surface* impunctate or partly punctate; abdomen not pubescent; prosternal process usually simple, but margined and tuberculate at apex in *bufo*. *Legs:* hind tibiae not sulcate along extreme outer edges; 4th hind-tarsal segment emarginate or moderately lobed; 5th hind-tarsal segment without obvious accessory setae, but sometimes (at least in some *fortellum*) with minute rudimentary ones (as in many other New Guinean Agonini). *Secondary sexual characters* normal. *Male copulatory organs* as figured (Figs. 64–66).

Genotype. *Fortagonum fortellum* n. sp. (below).

Generic distribution. High mountains of New Guinea.

Notes. This is an apparently natural group of surprisingly diverse species, of which many more probably remain to be discovered at high altitudes on different mountain ranges.

Key to the Species of Fortagonum

1. Prothoracic margins very wide anteriorly as well as posteriorly; elytral margin rounded at humeri; elytra purplish; (form very broadly subquadrate; eyes small but very abruptly prominent) (p. 248). . . . *limum*
– Prothoracic margins very narrow anteriorly, very wide only posteriorly; elytral margins abruptly angulate at humeri; elytra not purplish; (form and eyes variable). 2
2. Eyes small and scarcely more prominent than genae; mandibles long, slender, only slightly arcuate. 3
– Eyes small but rather prominent, much more so than genae; mandibles variable but never so produced as above. 4
3. Rather broadly subparallel; basal margin of elytra entire (p. 249). . *forceps*
– Oval-fusiform; basal margin of elytra joining bases of 3rd striae, obliterated inwardly (p. 250). . . . . *cychriceps*
4. Posterior supraocular setae present; form moderately broad, not fusiform (p. 251). . . . . *fortellum*
– Posterior (as well as anterior) supraocular setae absent; form very broadly rounded-fusiform (p. 252). . . . . *bufo*

FORTAGONUM LIMUM n. sp.

Description. With characters of genus as described above. Very broadly subquadrate; elytra inconspicuously purplish, not iridescent; upper surface (at 54×) finely and sparsely punctulate, with some additional coarser but rather superficial punctation on lateral margins of prothorax; microsculpture normal. *Head* relatively small but with neck thick and swollen; head about .47 width prothorax; mandibles not especially elongate; eyes small but excessively prominent; front conspicuously, irregularly, transversely impressed between eyes, and anterior frontal impressions extending backward into very deep channels above and behind eyes. *Prothorax* very wide; width/length about 1.78; base/apex about 1.33; sides strongly rounded for most of length, becoming nearly straight near base; posterior angles obtuse, slightly blunted; lateral margins very wide anteriorly as well as posteriorly, moderately reflexed; disc with light median line and vague transverse impressions. *Elytra* broad and relatively short, rather strongly convex; humeri broad but prominently rounded rather than pointed; basal margin entire, rounded rather than angulate at humeri; sides straight and probably subparallel to behind middle, then strongly arcuate to distinct but not strong subapical sinuations; apices rather narrowly independently rounded; intervals a little convex, not much modified toward apex; marginal (10th) interval narrow and poorly defined; 3rd interval impunctate on left elytron, 1-punctate (just behind middle) on right one. *Lower surface* impunctate or nearly so, but epipleurae roughened. *Legs:* 4th hind-tarsal segment with moderate outer and much shorter inner lobe. *Measurements:* length 11.0; width about 4.8 mm.

Type. Holotype ♀ (M.C.Z. No. 28,683) from Mt. Misim, Morobe Dist., **N-E. N. G.**, altitude and date not given (Stevens).

Measured specimen. The type.

Notes. The single specimen of this species is partly crushed, with the prothorax split lengthwise, so that the measurements and proportions given are only approximate. The species has the generic characters of *Fortagonum* and is probably related to the other species here placed in that genus, but it differs from all the others in a number of striking characters: color of elytra, excessive prominence of eyes, form of front of head, form of prothorax (with margins very wide anteriorly as well as posteriorly), and form of humeri (rounded rather than pointed).

FORTAGONUM FORCEPS n. sp.

Description. With characters of genus as described above. Rather broadly subparallel; upper surface impunctate except very finely and sparsely punctulate, rather shining, elytra somewhat iridescent in strong light only; microsculpture normal, with elytral meshes very fine and transverse. *Head* .57 & .56 width prothorax; mandibles unusually long, slender, and only slightly arcuate; eyes small and only slightly more prominent than genae; latter about as long as eyes, convex in profile; front moderately convex, more or less impressed transversely between eyes, with anterior impressions moderate and extending vaguely backward above eyes but not forming deep channels there. *Prothorax:* width/length 1.28 & 1.35; base/apex about 1.33 & 1.35; sides rather weakly arcuate for much of length, straighter posteriorly; posterior angles a little obtuse, narrowly rounded; lateral margins relatively narrow anteriorly, very wide posteriorly, flat, only slightly reflexed; disc with median line moderately impressed, transverse impressions almost obsolete. *Elytra* broad and rather short, only a little more than normally convex; basal margin entire, strongly advanced and acute at humeri; subapical sinuations faint or absent; apices rather narrowly, more or less conjointly rounded (a little more independently rounded in the ♀ paratype); intervals moderately convex, not much modified toward apex; an extra (10th) interval present for much of elytral length, moderately wide, flat or slightly convex; 3rd interval impunctate. *Male copulatory organs:* Fig. 64. *Lower surface* impunctate. *Legs:* 4th hind-tarsal segment emarginate, not lobed. *Measurements:* length 12.4; width 4.8–4.9 mm.

Types. Holotype ♂ (Leiden Mus.) and 1 ♀ paratype (M.C.Z. No. 28,684) both from Moss Forest Camp, Snow Mts., **Neth. N. G.**, 2,600–2,800 m. (about 8,450–9,100 ft.), Oct. 9–Nov. 5, 1938 (Toxopeus)

Measured specimens. The types.

Notes. Sufficiently compared with other species in the key above. This and the following species (*cychriceps*) are unique among New Guinean Agonini in the form of their mandibles which may be adapted to feeding on small snails or some other special food. The present species, except that it is larger, superficially resembles *F. fortellum* (below) of the Bismarck Range, but *fortellum* has approximately normal mandibles and differs in other technical details.

FORTAGONUM CYCHRICEPS n. sp.

Description. With characters of genus as described above. Oval-fusiform; upper surface virtually impunctate except lateral margins of prothorax vaguely punctulate; shining, head and pronotum opalescent or slightly iridescent, elytra more iridescent; microsculpture normal on head, very fine, transverse, and scarcely visible at 54× on pronotum and elytra. *Head* relatively long and narrow, .48 width prothorax; mandibles long, slender, only weakly arcuate; eyes small, scarcely more prominent than genae; latter about as long as eyes, only faintly convex in profile; front convex, obliquely flattened above eyes, with slight, almost indistinct frontal impressions. *Prothorax* widest very near base, strongly narrowed anteriorly; width/length 1.27; base/apex about 1.8; sides weakly arcuate for whole length; posterior angles would be right except narrowly rounded; lateral margins very narrow anteriorly, very wide basally, even less reflexed (more nearly in plane of disc) than in other species of genus; disc more convex than usual, with median line lightly impressed, transverse impressions almost obsolete. *Elytra* relatively longer than in other species of genus, rather gradually tapering posteriorly, more convex than usual; basal margin reaching and joining ends of 3rd striae but obsolete inwardly, strongly advanced and acute at humeri; sides almost evenly rather weakly arcuate from humeri to apices, without subapical sinuations; apices somewhat independently rounded; striae deeper and intervals more convex than usual; outer intervals not much modified toward apex; marginal (10th) interval present for most of elytral length, rather wide especially posteriorly, nearly flat; 3rd interval impunctate. *Lower surface* virtually impunctate. *Legs:* 4th hind-tarsal segment emarginate, not lobed. *Measurements:* length 11.5; width 4.3 mm.

Type. Holotype ♀ (Leiden Mus.) from Mist Camp, Snow Mts., **Neth. N. G.**, 1,800 m. (about 5,850 ft.), Jan. 1939 (Toxopeus); unique.

Measured specimen. The type.

Notes. Adequately characterized and compared with other species in the key above.

FORTAGONUM FORTELLUM n. sp.

Description. With characters of genus as described above. Not fusiform (Fig. 14); upper surface impunctate (except elytral intervals sparsely punctulate at 54×), moderately shining, elytra faintly iridescent in strong light only; microsculpture normal except so fine as to be scarcely visible on elytra. *Head* rather small and narrow, .54 & .55 width prothorax; mandibles not especially long; eyes rather small, moderately prominent; genae about as long as eyes, oblique; front almost evenly convex, with very slight anterior impressions. *Prothorax* widest behind middle, strongly narrowed in front, much less so behind; width/length 1.41 & 1.44; base/apex 1.47 & 1.42; sides broadly, almost evenly arcuate for whole length, or sometimes vaguely straighter both anteriorly and posteriorly; posterior angles a little obtuse, narrowly rounded; lateral margins relatively narrow anteriorly, very wide posteriorly, flat, scarcely reflexed; disc with middle line light, transverse impressions virtually obsolete. *Elytra* broad and rather short but otherwise of nearly normal outline in tribe; sides slightly arcuate at middle, more strongly so apically; disc a little more than normally convex; basal margin entire, about rectangular at humeri; subapical sinuations absent; apices conjointly rounded to obtuse, blunted, slightly dehiscent sutural angles; intervals flat or slightly convex, very variable toward apex, outer ones sometimes not much modified, or 8th and 9th and sometimes others deeply longitudinally impressed toward apex; variable short fragment of extra 10th interval present in some specimens absent in others, when present, convex and sharply defined, at outer apical curve of elytron; 3rd interval variably punctate (*e.g.* type has left 3rd interval normally 3-punctate except middle puncture is farther forward than usual, right 3rd interval 3-punctate with all punctures at 2nd stria; second measured specimen has left 3rd interval 2-punctate with punctures at 2nd stria about 2/5 from base and 1/4 from apex, and right 3rd interval 1-punctate with puncture at 2nd stria about 1/3 from base). *Lower surface* with sides of sterna superficially punctate. *Legs:* 4th hind-tarsal segment emarginate, not lobed. *Male copulatory organs* as figured (Fig. 65). *Measurements:* length 8.8–10.8; width 3.7–4.4 mm.

Types. Holotype ♂ (M.C.Z. No. 28,685) and 53 paratypes all from Mt. Wilhelm, Bismarck Range, **N-E. N. G.**, 7,000–10,000 ft., Oct. 1944 (Darlington), taken in and under various cover on the ground in heavy forest.

Measured specimens. The ♂ holotype and 1 ♀ paratype.

Notes. This is, of course, a thoroughly characterized species, distinguished from others in the key above. The variation in form of the outer elytral intervals (variably impressed or not impressed), in presence or absence of a variable fragment of a 10th interval, and in punctures of the 3rd interval is amazing, but the variation is erratic, with the different characters not correlated, and the whole series is from a limited area of continuous forest and has the look and in many ways the characters of a single population, which I have no doubt it is.

FORTAGONUM BUFO n. sp.

Description. With characters of genus as described above. Very broadly oval, very convex; upper surface virtually impunctate, only moderately shining, not iridescent; microsculpture normal. *Head* .49 & .51 width prothorax; mandibles somewhat longer and straighter than usual, but less so than in *forceps* and *cychriceps*; eyes small, rather prominent, but much less so than in *limum*; genae short and oblique; front convex, with slight anterior impressions. *Prothorax* widest in basal half, strongly narrowed anteriorly, not or scarcely so posteriorly; width/length 1.52 & 1.48; base/apex about 1.73 & 1.56; sides slightly sinuate behind anterior angles, then moderately arcuate, then straighter and subparallel toward base; basal angles nearly right, blunted; lateral margins very narrow anteriorly, very wide posteriorly, strongly flattened posteriorly but scarcely reflexed; disc strongly convex, with middle line moderately impressed, transverse impressions almost obsolete. *Elytra* widest well behind humeri, very convex, with strongly rounded sides; basal margin entire, a little obtusely (almost rectangularly) angulate at humeri; subapical sinuations slight or virtually absent; apices rather abruptly rounded (almost subangulate) about opposite 2nd striae, with sutural angles obtuse; striae rather deep; intervals moderately convex, not much modified toward apex; no distinct extra (10th) interval; 3rd interval impunctate. *Lower surface* with sides of mesosternum rather lightly punctate. *Legs:* 4th hind-tarsal segment with a moderate outer and slightly shorter inner lobe. *Male copulatory organs:* Fig. 66. *Measurements:* length 10.4–11.3; width 5.0–5.2 mm.

Types. Holotype ♂ (Leiden Mus.) and 1 ♀ paratype (M.C.Z. No. 28,686) both from Mist Camp, Snow Mts., **Neth. N. G.**, 1,800 m. (about 5,850 ft.), Jan. 1939 (Toxopeus).

Measured specimens. The types.

Notes. This species is unique among New Guinean Agonini in form as well as in absence of both pairs of supraocular setae.

PLATES

PLATE 1[1]

Fig. 1. *Tarsagonum latipes* new genus and species.
Fig. 2. *Notagonum externum* new genus and species.
Fig. 3. *Plicagonum fulvum* new genus and species.
Fig. 4. *Lithagonum annulicorne dilutior* new genus and subspecies.
Fig. 5. *Iridagonum quadripunctum* new genus and species.
Fig. 6. *Altagonum caducum* new genus and species.
Fig. 7. *Maculagonum pox* new genus and species.
Fig. 8. *Potamagonum diaphanum* new genus and species.
Fig. 9. *Gastragonum terrestre* new genus and species.
Fig. 10. *Idiagonum asperum* new genus and species.
Fig. 11. *Montagonum toxopeanum* new genus and species.
Fig. 12. *Nebriagonum cephalum* new genus and species.
Fig. 13. *Laevagonum cistelum* new genus and species.
Fig. 14. *Fortagonum fortellum* new genus and species.

Fig. 15. Right middle tarsus (from above, with bristles omitted) of *Tarsagonum latipes* (♀ paratype).

Fig. 16. Right 4th hind-tarsal segment (from above, with bristles omitted) of *Tarsagonum latipes*, with "a long outer lobe but almost no inner one" (♀ paratype).

Fig. 17. Same of *Euplenes apicalis*, "with 2 long, nearly equal lobes" (♀ paratype from Dobodura).

Fig. 18. Same of *Notagonum externum*, with "moderate outer and shorter inner lobe" (♀ paratype from Dobodura).

Fig. 19. Same of *Notagonum subpunctum capitis*, with apex "simply emarginate, not lobed" (♀ paratype).

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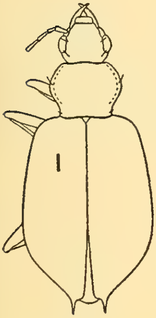
[1] Figures are to different scales; see descriptions for sizes of insects.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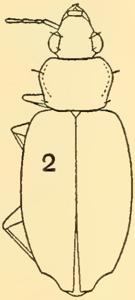
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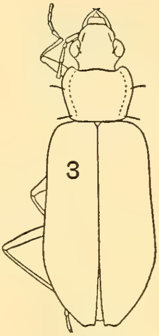
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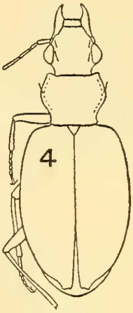
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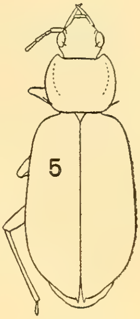
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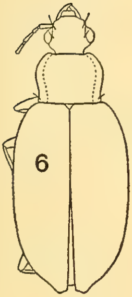
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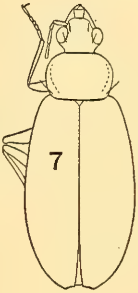
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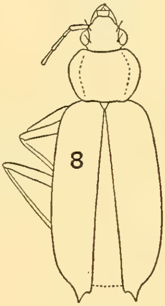
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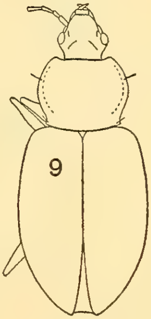
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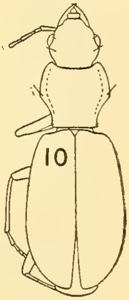
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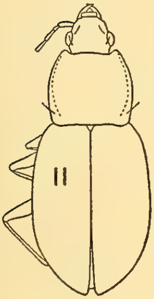
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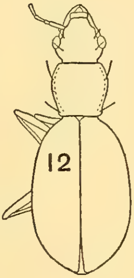
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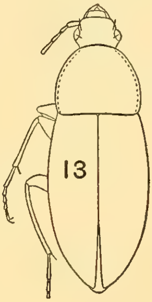
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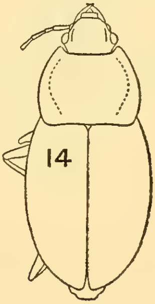
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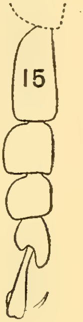
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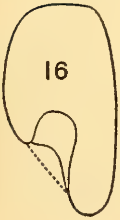
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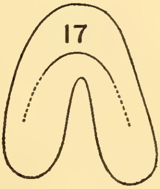
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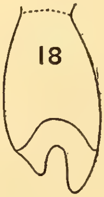
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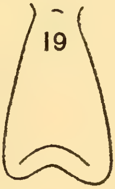
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PLATE 2

Fig. 20. Male copulatory organs (middle lobe from left, parameres from below, detached) of *Arhytinus major* (type).

Fig. 21. Same of *Tarsagonum latipes* (type).

Fig. 22. Same of *Euplenes apicalis* (type).

Fig. 23. Same of *Dicranoncus queenslandicus* Sl. (Guadalcanar Is.).

Fig. 24. Same of *Lorostemma informalis* (type).

Fig. 25. Same of *Notagonum angustellum* (type).

Fig. 26. Same of *Notagonum reversior* (type).

Fig. 27. Same of *Notagonum externum* (paratype).

Fig. 28. Same of *Notagonum vaporum* (type).

Fig. 29. Same of *Notagonum gibbum* (paratype).

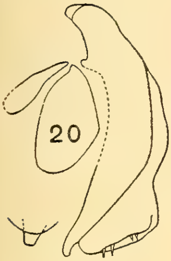
Fig. 30. Same of *Notagonum dentellum* (type).

Fig. 31. Same of *Notagonum malkini* (type).

Fig. 32. Same of *Notagonum subrufum* (type).

Fig. 33. Same of *Notagonum spinulum* (type).

Fig. 34. Same of *Colpodes violaceus* Chd. (Dobodura).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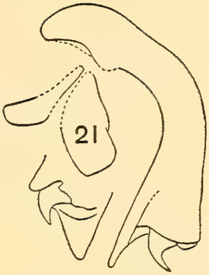
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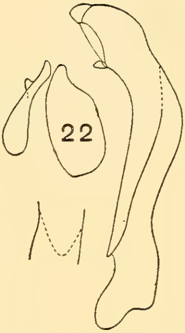
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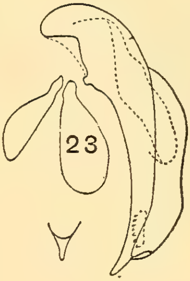
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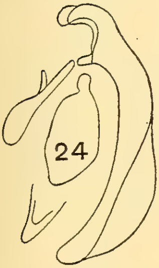
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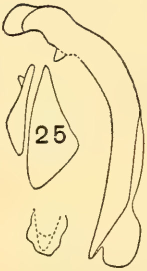
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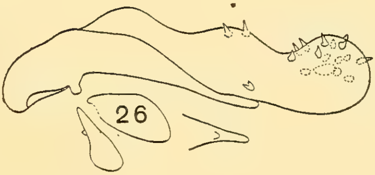
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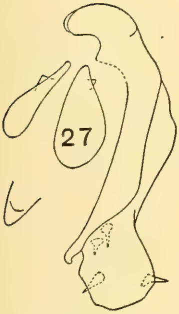
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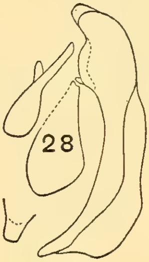
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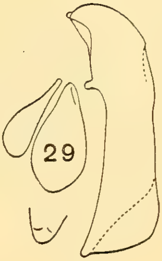
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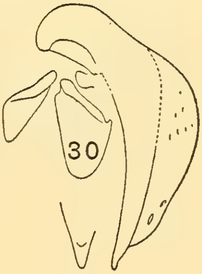
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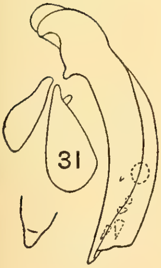
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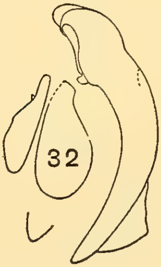
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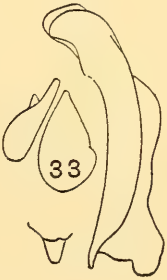
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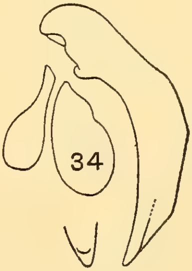
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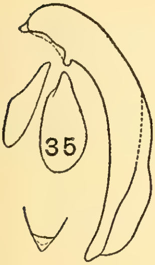
PLATE 3

Fig. 35. Same of *Colpodes helluo* (type).
Fig. 36. Same of *Colpodes laetus* Er. (Dobodura).
Fig. 37. Same of *Colpodes habilis* Sl. (Wasian).
Fig. 38. Same of *Colpodes antedens* (type).
Fig. 39. Same of *Colpodes acuticauda* (paratype).
Fig. 40. Same of *Colpodes sinuicauda* (type).
Fig. 41. Same of *Plicagonum rugifrons* (type).
Fig. 42. Same of *Plicagonum fulvum* (paratype).
Fig. 43. Same of *Lithagonum annulicorne dilutior* (type).
Fig. 44. Same of *Iridagonum quadripunctum* (type).
Fig. 45. Same of *Iridagonum subfusum* (type).
Fig. 46. Same of *Altagonum vallicola* (type).
Fig. 47. Same of *Altagonum magnox* (type).
Fig. 48. Same of *Altagonum caducum* (paratype, Mt. Misim).
Fig. 49. Same of *Altagonum sphodrum* (type).
Fig. 50. Same of *Altagonum paralimbus* (type).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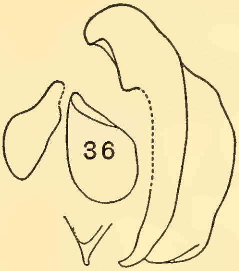
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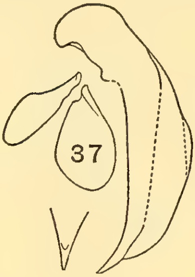
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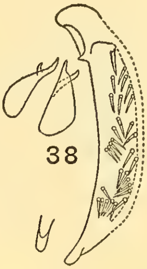
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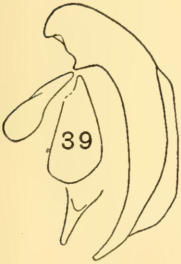
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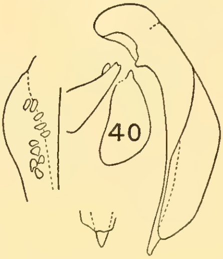
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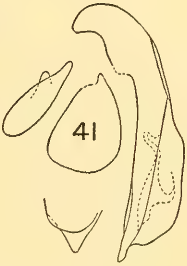
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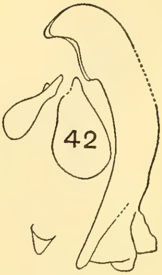
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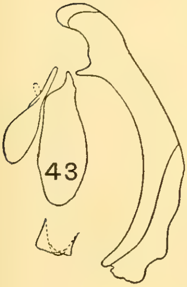
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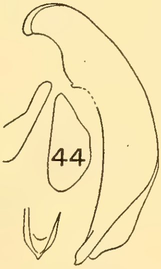
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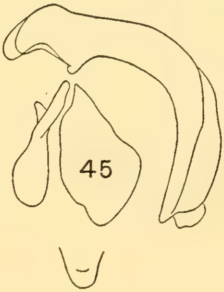
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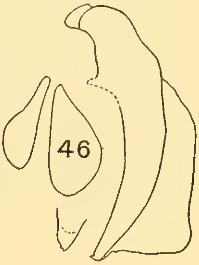
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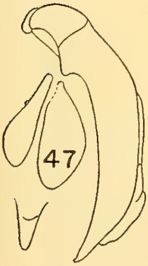
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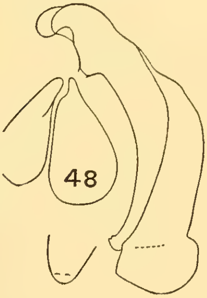
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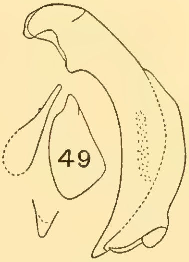
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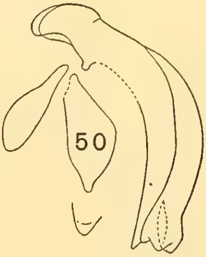
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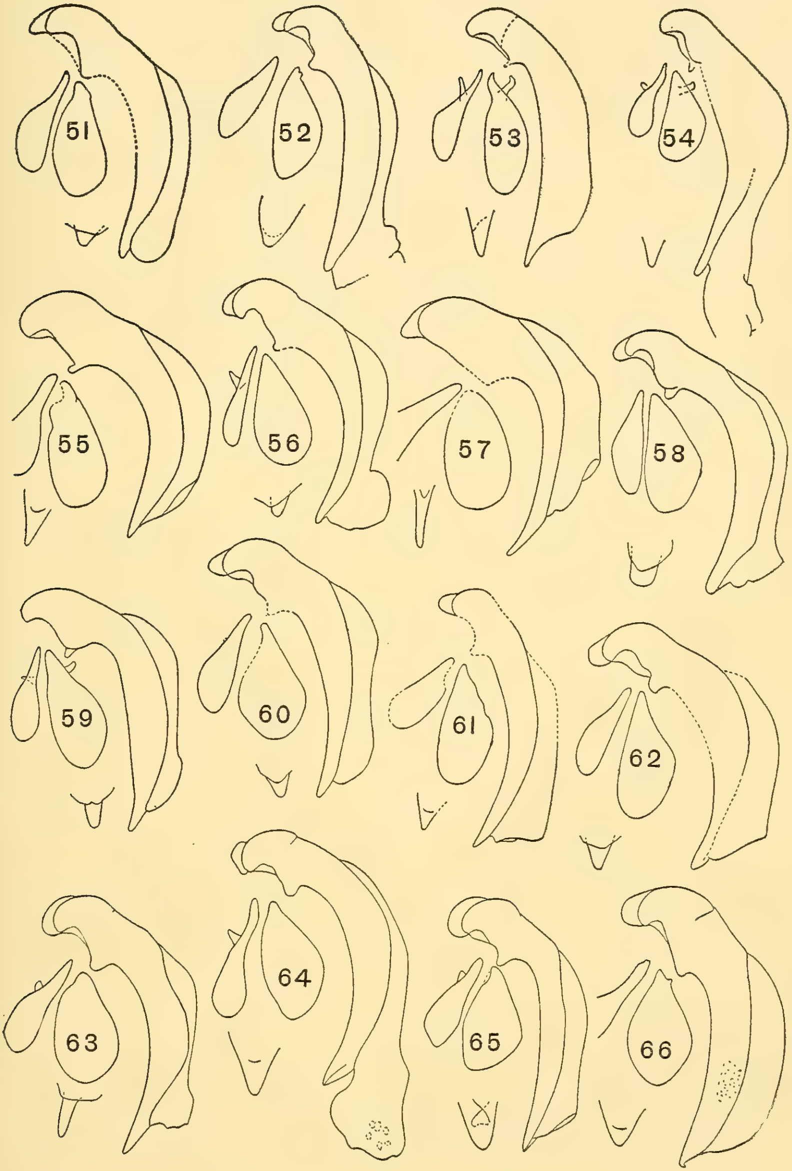
PLATE 4

Fig. 51. Same of *Altagonum nudicolle* (type).
Fig. 52. Same of *Maculagonum setipox* (type).
Fig. 53. Same of *Potamagonum diaphanum* (type).
Fig. 54. Same of *Gastragonum laevisculptum* (type).
Fig. 55. Same of *Gastragonum subrotundum* (type).
Fig. 56. Same of *Gastragonum terrestre* (type).
Fig. 57. Same of *Idiagonum asperum* (paratype).
Fig. 58. Same of *Montagonum toxopeanum* (paratype).
Fig. 59. Same of *Nebriagonum cephalum* (type).
Fig. 60. Same of *Nebriagonum transitior* (type).
Fig. 61. Same of *Laevagonum subcitum* (type).
Fig. 62. Same of *Laevagonum citum* (type).
Fig. 63. Same of *Laevagonum cistelum* (paratype).
Fig. 64. Same of *Fortagonum forceps* (type).
Fig. 65. Same of *Fortagonum fortellum* (paratype).
Fig. 66. Same of *Fortagonum bufo* (type).



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AT HARVARD COLLEGE
Vol. 107, No. 4

REVISION OF THE SPECIES CURRENTLY REFERRED TO ALEPOCEPHALUS, HALISAURICEPS, BATHYTROCTES AND BAJACALIFORNIA WITH INTRODUCTION OF TWO NEW GENERA

By A. E. Parr
American Museum of Natural History

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
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September, 1952

No. 4. — *Revision of the Species Currently Referred to Alepocephalus, Halisauriceps, Bathytroctes and Bajacalifornia With Introduction of Two New Genera*

By A. E. Parr

The discovery of a second specimen of *Bathytroctes nasutus* in the collections made by the "Atlantis" off Cuba, and now deposited in the Museum of Comparative Zoology, has provided an opportunity to re-examine more closely the relationships within the genus *Bathytroctes* as a whole, with the result that it now seems possible to effect several desirable subdivisions of the very heterogeneous assembly of species heretofore included in *Bathytroctes*.

The collections of the Museum of Comparative Zoology also contain the types of several species of both *Alepocephalus* and *Bathytroctes*, which have not been redescribed since they were first introduced into the literature by Garman in 1899, and are therefore in need of redefinition in order to bring their identification up to date in relation to the other species known today. This would seem to be most easily accomplished by the publication of new keys to the genera involved, without burdening this account with the detailed redescriptions of the species, which will form part of a monograph on the Alepocephalidae now being prepared by the writer.

In regard to *Alepocephalus asperifrons* Garman 1899 (p. 291, pl. LIX, fig. 1), type No. 28472 M.C.Z., this has already (Parr, 1951, p. 8) been made the type of a new genus, *Bruunichthys*. The other species of *Alepocephalus* described by Garman may be identified by the use of the following key, which extends to the species of this genus the revised key to the genera of the Alepocephalidae given by Parr, 1951, pp. 4–10.

The functions used to express the proportions in per cent of the length without caudal fin, identified by the letter L, are those introduced and explained by Parr, 1949. To find the indicated minimum size of the head of a specimen of *A. umbriceps* of 250 mm. L, according to the key, solve the function (39.5 − .015L) as follows:

$$39.5 - .015 \times 250 = 39.5 - 3.75 = 35.75$$

The head should be more than 35.75 per cent of L.

If the head of the specimen is less than the minimum indicated for *A. umbriceps*, e.g. 33.9 per cent of L, one may, for comparison with *umbriceps*, estimate a corresponding formula for the specimen in one of the following ways.

Either indirectly, by subtracting 33.9 from the value (35.75) which the formula gave as a minimum for *umbriceps* at 250 mm. L, and subsequently subtracting (adding if the head of the specimen had been larger than in *umbriceps*) this difference (1.85) from the constant (39.5) of the *umbriceps* formula. This gives the corresponding formula for the head of the specimen as (37.65 − .015L) per cent of L.

Or directly, by solving the function for *umbriceps* for the measurements of the specimen, treating the constant of the function as the unknown, K, as follows:

$$(K - .015 \times 250) = 33.9$$

$$K = 33.9 + .015 \times 250 = 33.9 + 3.75 = 37.65$$

which gives the head of the specimen as:

$$(37.65 - .015L) \text{ per cent of } L.$$

Note that this does not establish the actual formula for the species to which the specimen belongs. It only establishes a possible basis for comparison with *umbriceps* in purely descriptive terms. If the species is closely related, and the formula for *umbriceps* is well established empirically, either for the species (as it is not in this case), or as an approximate descriptive generalization for the genus (which applies here) it is likely that the new formula will also be approximately valid for the new species, but for one specimen it only offers a method of evaluating the difference from *umbriceps* at the size of the specimen under consideration.

Key to the genus Alepocephalus

A. Anal fin long, with 28–32 rays, 8–11 rays more than in dorsal fin. Anal fin base 20–24 per cent of L, or 5–9 per cent of L longer than dorsal fin base. Heads very small, less than (35.5 − .025 L), with an average of about (34.5 − .03 L) per cent of L. Orbits small, less than (12 − .027 L), average about (11 − .027 L) per cent of L. Snout short. Fins advanced, snout to V 46–50, snout to D 62–66, snout to A 62.5–66.5 per cent of L. 61–63 scales in longitudinal series. Only 8–11 simple pyloric caeca. . . . . *Lloydiella*, new subgenus

Genotype: *Alepocephalus bicolor* Alcock 1892

B. Anal fin moderate to short, with 16–25 rays, not in excess of 4 rays more than in dorsal fin. Anal fin base only 12–19 per cent of L, and less than 5 per cent of L longer than base of dorsal fin. Heads more than (34.4 − .025 L), generally from (35.5 − .025 L) to (44 − .015 L) per cent of L. Orbits not less than (9 − .008 L) per cent of L. Snout to V 46–61, snout to D 65–76, snout to A 66–74 per cent of L.

  I. A long and pointed snout formed by the upper jaws extends beyond the point of lower jaw by more than 3 per cent of L. Length of snout about (15 − .006 L) per cent of L, or more. Vertical fins very posterior, distance from snout to both dorsal and anal fin (according to figure) about (72.5 + .01 L) per cent of L. Only 7 "rudimentary" pyloric caeca . . . . Subgenus *Halisauriceps* (Fowler 1934)

  A. longiceps Lloyd 1909

II. Snout short and blunt, its length less than (13 – .006 L) per cent of L, its tip not extending beyond the point of lower jaw by more than one per cent of L, measured horizontally. One of the distances from snout to dorsal or to anal fin always less than (70 + .01 L) per cent of L, both distances usually less than this value and always less than (72 + .01 L) per cent of L. . . . . Subgenus *Alepocephalus* (Risso 1820)

- a. Only 40–60 scales in a longitudinal series.
  - 1. Distance from snout to anal fin 5–8 per cent of L longer than snout to dorsal. Only 9–10 simple pyloric caeca. Anal fin with 17–20 rays, its base 12–13 per cent of L. Head moderate, about (38 – .015 L) per cent of L. Orbit small, (10.2 – .008 L) per cent of L. Mouth small, upper jaws only about (11 – .008 L) per cent of L, lower jaws less than (16 – .008 L) per cent of L. . . . . *A. andersoni* Fowler 1934
  - 2. Distance from snout to anal fin less than 3 per cent of L longer than snout to dorsal. 15–23 pyloric caeca.
    - x. Anal fin with 20–24 rays, its base 17–20 per cent of L. 19–23 pyloric caeca. Heads more than (36 – .018 L) but less than (38 – .15 L) per cent of L. Orbits about (12.4 – .008 L) per cent of L. Mouth moderate, upper jaws less than (12 – .002 L), lower jaws not more than about (18 – .008 L), but more than (15 – .008 L) per cent of L. . . . . *A. rostratus* Risso 1820
    - xx. Anal fin with 16–20 rays, its base 12–15 per cent of L. 15–17 pyloric caeca.[1]
      - y. Head and eyes small, head about 27–28, corresponding to (33.4 – .018 L) or (35.5 – .025 L) per cent of L, eye only about 7–7.2, corresponding to about (9.6 – .008 L) per cent of L, at 310 mm. L. . . . . *A. owstoni* Tanaka 1908
      - yy. Head large, more than (37 – .018 L), orbits more than (11 – .008 L) per cent of L.
        - z. Eyes moderate, orbits less than (12.5 – .008 L) per cent of L. . . . . . . *A. australis* Barnard 1923
          - 1. Head large, from about (39 – .015 L) to (41 – .015 L) per cent of L. . . . . *A. australis australis* (Barnard 1923)
          - 2. Head moderate, less than (39 – .015 L) per cent of L. . . . . *A. australis barnardi* (Norman 1930)
        - zz. Eyes large, orbits about (14 – .008 L) per cent of L. Head large, corresponding to about (41.5 – .015 L) per cent of L. . . . . *A. macrops* Lloyd 1909

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[1] Not known for *A. owstoni*.

b. About 64–70 scales in a longitudinal series. Snout to dorsal fin from 3 per cent of L shorter to 5 per cent of L longer than snout to anal fin. 13–19 pyloric caeca.

  1. Anal fin with 21–25 rays, its base 15–20 per cent of L. D, 20–23. Distance from snout to ventrals 46–51.5, snout to dorsal 65–69, and snout to anal fin 66–71.5 per cent of L. Head small, less than (39.5 – .015 L) per cent of L...... ....*A. bairdi* Goode and Bean 1879

  2. Anal fin with only 17–19 rays, its base only 12–15 per cent of L. D, 16–18. Distance from snout to ventrals 54–58, snout to dorsal 69.5–72.5, snout to anal fin 71–73 per cent of L.

    x. Head small, less than (39.5 – .015 L) per cent of L.... ....*A. blanfordi* Alcock 1892[1]

    xx. Head large, more than (39.5 – .015 L) per cent of L.

      y. Upper jaw reaches approximately to below the middle of the orbit, being nearly 5 per cent of L longer than the snout. Suboperculum with two distinct ridges ending posteriorly in two separate points. 18 pyloric caeca............................ ....*A. umbriceps* Jordan and Thompson 1914

      yy. Upper jaws ending distinctly in advance of the centers of the orbits, being less than 3 per cent of L longer than the snouts. Suboperculum ends in a single rounded point, and has only a single ridge. 14–15 pyloric caeca........*A. productus* Gill 1883

c. 80–105 scales in a longitudinal series.

  1. Head large, more than (41.5 – .017 L) per cent of L. 21–24 long, simple pyloric caeca. Width of skull more than (14 – .0028 L) per cent of L. Upper jaws more than (16 – .008 L) per cent of L[2]......................... ....*A. agassizi* Goode and Bean 1882

  2. Head moderate, less than (40 – .017 L) per cent of L. Only 12–16 long, simple pyloric caeca. Width of skull not more than (14 – .0080 L) per cent of L. Upper jaws less than (14 – .002 L) per cent of L.[2]

    x. 15–16 scales between lateral line and origin of dorsal fin. Upper jaws not more than (12 – .002 L), not less than (11 – .002 L) per cent of L. Head less than (37.5 – .018 L), width of skull not more than (12.5 – .008 L) per cent of L. Suboperculum irregularly quadrangular, with a broad, sloping posterior margin, and without distinct main ridge .... *A. tenebrosus* Gilbert 1891

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[1] It is very uncertain whether *A. blanfordi* is actually distinct from *A. productus*. The type of the former is no longer available, and only the statement that its head is one-third of the length of the body permits a tentative distinction to be made, until new material may be obtained.

[2] Note the changes in coefficients of slope between *A. agassizi* and the other species under c, in regard to widths of skull (.0028 compared with .008) and lengths of upper jaw (.008 compared with .002). These formulas can, however, only be taken as purely descriptive of the data now available which are quite insufficient for the establishment of definitive norms.

xx. Only 10–12 scales between lateral line and origin of dorsal fin. Upper jaws not less than (12 − .002 L) per cent of L. Suboperculum with distinct main ridge ending in a point at the posterior margin.

  y. Head more than (38.5 − .017 L), width of skull about (13.7 − .008 L) per cent of L. Suboperculum narrow, sickle-shaped, ending posteriorly in a single point. Center of anus about one-third as far from the origin of anal fin as from the bases of anterior ventral finrays .... *A. fundulus* Garman 1899

  yy. Head less than (36 − .018 L), or possibly less than (37.5 − .025 L), width of skull about (12 − .008 L) per cent of L. Suboperculum wide, but with a short, blunt, point in the posterior outline at the end of the main ridge. Center of anus not more than one-fourth as far from the origin of anal fin as from the bases of anterior ventral finrays...... .... *A. convexifrons* Garman 1899

LLOYDIELLA new subgenus

The long anal fin separates *A. bicolor*, in an easily defined manner, from all other species of *Alepocephalus*. Actually *A. bicolor* would seem to be at least equally, if not more, unique with reference to several other features which cannot be quite so simply and easily expressed. In scatter diagrams showing proportions in reference to absolute length the measurements of *A. bicolor* form a group entirely apart from the rest in regard to the length of the head and of the lower jaw; almost entirely apart with regard to the orbits, interorbital width, and the lengths of the upper jaws; and largely apart in regard to the width of the skull and the distances from the snout to dorsal and anal fin. Characteristic of the groups of measurements for which a trend of change with size can be fairly clearly established, is the fact that the coefficients of slope for the *A. bicolor* are much greater than those that seem indicated for any other species of *Alepocephalus*. Thus the average size of the head in *A. bicolor* may be fairly expressed as (34.5 − .03 L) per cent of L, while no other species of which there is enough material available gives indications of a coefficient of change greater than −.018L. Similarly the orbits and lower jaws of *A. bicolor* indicate a coefficient of −.027L, while the measured orbits and lower jaws of all other species are in fair agreement with coefficients of −.008L, or less.

While the proportions dealt with in the preceding paragraph might be viewed as only partly independent and partly dependent upon the size of the head, this cannot be said of the relationships of the interorbital width to the diameter of the orbit and to the width of the skull. In both subspecies of *A. bicolor* the interorbital widths expressed in per cent of the diameter of the orbit, and also in per cent of the width of the skull, clearly indicate a coefficient of change of both percentages of about +.2L. In all other species of *Alepocephalus* of which there are a reasonable number of measurements, the changes with size of the same percentages are well fitted by a coefficient of only +.06L. This is specifically true of *A. tenebrosus* and *A. convexifrons,* two of the species that approach most closely to *A. bicolor* in regard to the size of both the orbits, and the length as well as the width of the head.

With so much concurrent evidence to indicate that *A. bicolor* occupies a quite separate position within the genus, at least a separate subgenus seems in order.

Subgenus HALSAURICEPS (Fowler 1934)

Genus *Halisauriceps* Fowler 1934, p. 247.

The new genus introduced by Fowler, 1934, was based solely upon the figure and brief description of *Alepocephalus longiceps* published by Lloyd, 1909. Unfortunately the type has been destroyed by accident, and no further information can be obtained about this species until fresh material is obtained.

The figure shows no indication of a shoulder organ, so one may reasonably assume that the species is a true alepocephalid. But nothing is known of the supramaxillaries, or of the manner in which the prominent snout is formed by the upper jaws, the extent of the possible modification of the premaxillaries and of their connection with each other, and other features that might be involved. Lloyd mentions "seven rudimentary caeca," which would be exceptional as a normal condition in a species of *Alepocephalus.* The present writer has several times found "rudimentary" caeca as an obviously abnormal condition of individual specimens, e.g. associated with parasites in the abdominal cavity or with unmistakable malformations. In some species of other genera, with only one or two caeca, these, although normal, may be so small that they might be described as rudimentary. But, with as many as seven caeca present, their rudimentary size or condition seems most likely to represent an individual abnormality. In certain instances of an obviously abnormal rudimentary condition of the caeca, there is also a strong indication that the number of discernible caeca may likewise have been reduced. It is therefore quite possible that the normal number of caeca in *A. longiceps* may be higher than seven.

It is thus evident that the actual status of *Halisauriceps* is quite obscure and must remain obscure until new material becomes available. The writer would hazard a guess that such material would serve to sharpen the distinction between *A. longiceps* and other alepocephalids, but, in the absence of factual knowledge, it seems best to retain the species within the genus in which it was just introduced, and in which its presently known features will still fit without broadening of the generic definition.

Bathytroctes and Related Genera

In the key to the genera of the Alepocephalidae previously published by the writer (Parr 1951, pp. 4–10) all the genera and subgenera dealt with in the following were still retained within a single genus, *Bathytroctes,* with a definition broad enough to cover the peculiarities of all of these forms. The following key may therefore be used as an extension of the previous key, starting after the point (*I, B, 2, b, xx, zz, yy, v*) on page 5, at which *Bathytroctes, sensu lato,* is defined.

In a scatter diagram showing the relative lengths of the heads plotted against absolute lengths of the bodies (L) for all specimens of all species here considered, those that have been previously referred to the genus or subgenus *Bajacalifornia,* plus *Bathytroctes calcaratus,* which also belongs here, form an exceptionally well defined and well separated group, with all species apparently fitted by a single formula: Length of head $(35.4 - .04L)^{+.5}_{-.4}$ per cent of L. The same coefficient of change also applies with unusual accuracy to the two known specimens of "*B.*" *nasutus,* as follows: head $(37.25 - .04L)^{\pm .05}$ per cent of L.

Among the rest of the species we also find two well separated groups, one with small, and one with large heads. Among the former we have only the measurements of single specimens of each species, so it is not possible to speak with confidence of the coefficient of slope that may actually apply to this group. But, using the coefficient of slope indicated for the species with large heads, we find that the measured lengths of the heads in the small-headed group do not exceed (35 − .03L) per cent of L, while the measured heads in the large-headed group all exceed (37.5 − .03L) and may even exceed (45 − .03L) per cent of L. It may be probable that the forms with smaller heads have a larger coefficient of slope, but even so, the measured heads would be less than (36.5 − .035L) and also less than (37.5 − .04L) per cent of L. On any assumption the small-headed species thus would seem to form a well separated group.

This separation of the small-headed group from those with large heads is confirmed by the position of the anus (at A, versus removed from A), agrees with very evident differences in general habitus which are not so easily defined in words, and greatly facilitates the general taxonomy of the group as a whole. A separate genus *Grimatroctes* is therefore introduced for these forms.

The separation of *Grimatroctes* from the large-headed species retained in *Bathytroctes* also makes it possible to re-establish the genus *Bajacalifornia*. In *Bathytroctes, sensu stricto* one may find various degrees of moderate development of a symphyseal knob, which, although it never compares with the symphyseal knobs in large specimens of *Bajacalifornia*, may even exceed the relative magnitude of the knob in smaller specimens such as those from which *Bajacalifornia drakei* is known. *Grimatroctes* on the other hand remains sharply distinct from *Bajacalifornia* in regard to symphyseal knob and the profile of snout and lower jaw. *Bajacalifornia* can thus be sharply distinguished from *Bathytroctes, sensu stricto,* by its very small head, and from *Grimatroctes* by the features first used to define *Bajacalifornia* as a separate genus.

The genus *Rinoctes* is so sharply distinct from the others by the shape and structure of its snout, that no confusion is possible. The fact that it agrees with *Bajacalifornia* in the formula for the length of the head, sharpens the distinction beyond any practical need by opposing the projecting snout of *Rinoctes* against the prominent lower jaw of *Bajacalifornia*.

Within the genus *Bathytroctes, sensu stricto, B. michaelsarsi* represents a species of strikingly different appearance from that of the others. This difference in general appearance is confirmed by entirely different gillraker, and pectoral fin ray counts, and a new subgenus, at least, would seem in order.

Key to genera of the Bathytroctes group

A. Head small, less than (37 − .035 L) per cent of L.

   1. Premaxillaries meet dorsally in a long and very firm, almost rigid symphysis closely and strongly joined by integuments, so as to form a hard, beak-like, pointed snout, projecting beyond the tip of lower jaw by more than 1 (about 1.3) per cent of L. Anus only one-half to two-thirds as distant from the insertion of the anterior ventral fin rays as from the origin of anal fin. Upper and lower jaws of approximately equal length, or upper jaws slightly longer. 6–8

pyloric caeca. 20–25 gillrakers in first arch. P. 8...............
....*Rinoctes*, new genus
Genotype: *Bathytroctes nasutus* Koefoed 1927

2. Premaxillaries do not form a prominent, pointed and beak-like snout, and are not joined in a long, almost rigid symphysis. Anus at anal fin, its centre about 3–15 times as distant from the insertion of anterior ventral fin rays as from the origin of anal fin.
   a. Symphysis of lower jaw with a prominent ventral knob, projecting forward beyond the vertical from the point of the snout, and continuing the dorsal profile of the head downward and forward. Head very small, not over $(36 - .040\ L)$ per cent of L. Eyes small, less than $(14 - .034\ L)$ per cent of L. Snout long, not less than $(50 + .4\ L)$ per cent of orbit. Length of lower jaw exceeds length of upper jaw by more than $(4 - .01\ L)$ per cent of L. 11–21 pyloric caeca. P. 13–17. About 50–65 scales in a longitudinal series....................................
   ....Genus *Bajacalifornia* Townsend and Nichols 1925
   b. Symphysis of lower jaw not prominent beyond the snout, with only a slight point ventrally. Eyes larger, more than $(14 - .034\ L)$ per cent of L. Snout shorter, not over $(75 + .1\ L)$ per cent of orbit. Jaws subequal or with lower jaw less than $(4 - .01\ L)$ per cent of L longer than upper jaw. 9–13 pyloric caeca. 32–38 gillrakers in first arch. 55–80 scales in a longitudinal series. P. 11–12. Measured heads not over $(35 - .030\ L)$ per cent of L....................*Grimatroctes*, new genus
   Genotype: *Bathytroctes grimaldi* Zugmayer 1911

B. Head large, more than $(37 - .030\ L)$ per cent of L. Anus removed from anal fin, its center from about one-third to twice as distant from the insertion of anterior ventral fin rays as from the origin of anal fin. Less than 60 (about 42–55) scales in a longitudinal series. No beak-like snout. Symphysis of lower jaw not greatly enlarged and prominent. 6–9 pyloric caeca.............................Genus *Bathytroctes* Günther 1878

RINOCTES new genus

Genotype *Bathytroctes nasutus* Koefoed 1927, p. 50, pl. III, fig. 10.

Diagnosis. No shoulder organ. Two supramaxillaries. Premaxillaries with continuous free edge. Interoperculum normal, elongate, oriented obliquely upwards and backwards, covered anteriorly by the preoperculum. Body completely scaly in the adults. No scales on head. Pectoral and caudal fins normal, without produced rays. Origin of dorsal fin well in advance of the origin of anal fin, which has less than 20 rays. Teeth in jaws in single series; dentition of maxillaries approximately equal to, or more extensive than that of the premaxillaries, which meet dorsally in a long, firm symphysis so as to form a hard, beak-like, pointed snout, projecting beyond the point of lower jaw by more than 1 per cent of L. Anus well in advance of the middle of the distance between the insertion of the anterior ventral fin rays and the origin of anal fin. 6–8 pyloric caeca. 20–25 gillrakers in first arch. Pectorals small, with only 8 rays. Head small, less than (37 − .035 L) per cent of L. The genus contains only one species.

RINOCTES NASUTUS Koefoed 1927

This species was originally described from a single specimen taken in the eastern portion of the Sargasso Sea, southwest of the Azores (N. 35°59′, W. 33°1′). It has not been reported again in the literature. It was therefore of considerable interest to find a second specimen in the collections of the Museum of Comparative Zoology (No. 35587) taken by the "Atlantis" inside of the Antillean chain of islands, off the south coast of Cuba, N. 20°47′, W. 80°24′, at Station 2966, February 26, 1938. The fact that both specimens were taken at extremely great depths, the type in 2865 meters, the "Atlantis" specimen in 3886 meters depth, suggests that we are here dealing with one of the most abyssal forms of living teleosts, since the records of alepocephalids of this general character plainly indicate that they belong to the bottom fauna, as explicitly recognized by Koefoed (1927) with whom the writer entirely agrees. On the assumption that the species may belong to the very great depths only, it is also of interest to note that the two specimens were taken in entirely separate ocean basins. Although the effectiveness of this separation must remain uncertain until the life history of the species is known, it does make it desirable to give the counts and measurements of the "Atlantis" specimen in some detail, as follows.

D. 14½. A. 12½. P. 8. V. 7. Br. 7. Gillrakers in first arch 4/1/15. Pyloric caeca 6 (2 + 4).

Length without caudal fin 122 mm. Proportions in per cent of length without caudal fin: Head 32.4. Orbit, longitudinally 9.1. Orbit, vertically 5.8. Snout 10.6. Snout to top of gill slit 29.1. Snout to top of preopercle 23.6. Interorbital width 2.95. Sphenotic width of skull 11.5. Pterotic width of skull 12.3. Combined length of upper jaws 17.1. Width of upper jaws (Max. + Supramax.) 3.3. Length of lower jaw 17.2. Length of premaxillary 5.9. Snout to dorsal fin 62.5. Snout to anal fin 74.5. Snout to ventrals 58.4. Base of dorsal 13.6. Base of anal fin 8.2. Insertion of ventral fins to center of anus 5.6. Greatest depth of body 13.9. Least depth of caudal peduncle 6.8. Longest gillraker 3.3. Longest pyloric caecum 5.3.

Stomach sipho-caecal, i.e. with a bluntly pointed end, extending beyond the pyloric arm by less than the diameter of the pyloric arm at the base.

It has, unfortunately, not been possible to obtain usable counts of the scales.

Genus BAJACALIFORNIA Townsend and Nichols 1925

Key to the species

A. Very slender, not over 10 scales in transverse count, about 50–55 in longitudinal series. Diameter of orbit more than (60 − .075 L) per cent of lower jaw. 21 pyloric caeca. Stomach siphonal. About 26 gillrakers in first arch, about 19 in lower limb. Western Atlantic. . . . . *B. drakei* Beebe 1929

B. Body deeper, 15–20 scales in transverse count.

  1. Only about 11 short pyloric caeca. Stomach siphonal. About 32 gillrakers in first arch, about 24 on lower limb. Diameter of orbit more than (60 − .075 L) per cent of lower jaw. 50–55 scales in longitudinal series. Pacific (Gulf of California) . . . . *B. burragei* Townsend and Nichols 1925
  2. 16–18 long pyloric caeca. Stomach caecal, with pyloric arm inserted in middle third of the combined length of caecum and ventricle. Diameter of orbit less than (55 − .075 L) per cent of lower jaw. About 60–62 scales in longitudinal series. 24–25 gillrakers in first arch, 18–19 on lower limb. Indo-Pacific. . *B. calcaratus* Weber 1913
     Syn.: *B. burragei* Norman 1939

GRIMATROCTES new genus

Genotype *Bathytroctes grimaldi* Zugmayer 1911a, p. 1; 1911b, p. 6, pl. I, fig. 2.

Diagnosis. No shoulder organ. Two supramaxillaries. Premaxillaries normal, with continuous free edge. Interoperculum normal, elongate, oriented obliquely upwards and backwards, covered anteriorly by the preoperculum. Body completely scaly in the adults. No scales on head. Pectoral and caudal fins normal, without produced rays. Origin of dorsal fin well in advance of the origin of anal fin, which has less than 20 rays. Teeth in jaws in single series; dentition of maxillaries approximately equal to, or more extensive than that of the premaxillaries, which are not joined dorsally in a firm symphysis and do not form a prominent, pointed snout. Anus at anal fin. Symphysis of lower jaw not prominent beyond the short snout, and with only a slight point ventrally. Head small, less than (37 − .035 L) per cent of L. Eyes large. 32–38 gillrakers in first arch. 9–13 pyloric caeca. 11–12 rays in pectoral fins. Scales small, 55–80 in a longitudinal series.

Key to the species of Grimatroctes

A. About 70–78 scales in a longitudinal series, 18–22 in transverse count. Pectoral fin bases completely surrounded by normal squamation in front and above, without naked band from gill opening to axil.
  1. Only 9 pyloric caeca. Orbit about (13.5 − .02 L) per cent of L. Br. 6 . . . . *G. grimaldi* (Zugmayer 1911)
  2. About 13 pyloric caeca. Orbit about (14.5 − .02 L) per cent of L. Br. 7 . . . . *G. microlepis* (Günther 1878)

B. About 55–61 scales in a longitudinal series, less than 18 in transverse count.
  1. Caudal peduncle deep, its depth (at 160 mm. L) about 10–11 per cent of L, and about one-half of the depth of the body at the shoulder. Sphenotic width of skull about (14.5 − .015 L); diameter of orbit (13.5 − .03 L) per cent of L. Width of skull at anterior end of orbit about 4.7 per cent of L . . . . *G. danae*, Parr 1951
  2. Caudal peduncle slender, its depth (at 220 mm. L) only about 6–6.5 per cent of L, and about one-third of the depth at the shoulder. Sphenotic width of the skull only about (13.3 − .015 L); diameter of orbit about (15.8 − .03 L) per cent of L. Width of skull at anterior end of orbit only about 3.4 per cent of L . . . . *G. zugmayeri* (Fowler 1934

Genus BATHYTROCTES Günther 1878

Key to the subgenera and species

A. Pectorals with 16–18 rays. 28–32 gillrakers in first arch, 20–23 in lower limb. 45–55 scales in longitudinal series . . . . *Nomoctes*, new subgenus
Genotype: *Bathytroctes michaelsarsi* Koefoed 1927

B. Pectorals with only 10–12 rays. Only 18–22 gillrakers in first arch, 13–15 in lower limb. 42–48 scales in longitudinal series . . . . Subgenus *Bathytroctes* (Günther 1878)
  1. Head moderate, less than (39.5 − .03 L), sphenotic width of skull less than (17 − .015 L) per cent of L.
    a. Anus somewhat nearer to the origin of anal fin than to the insertion of anterior ventral fin rays. Lower edge of premaxillaries highly arched in lateral view, upper part without lateral toothplates. Eyes large, diameter of orbit corresponds to (19 − .03 L) per cent of L. Articulation of lower jaw approximately below middle of orbit. Anterior supramaxillary extends forward well beyond posterior supramaxillary . . . . *B. inspector* Garman 1899
    b. Distance from the insertion of anterior ventral fin rays to center of anus only about ⅓–⅔ of distance from anus to anal fin. Premaxillary with a series of horizontal, semi-elliptic platelike

teeth along its upper portion, lower edge not highly arched. Eyes moderate, diameter of orbit less than (16 − .03 L) per cent of L. Articulation of lower jaw below posterior one-fourth of orbit. Anterior supramaxillary small, does not extend forward beyond posterior supramaxillary. . . . *B. alvifrons* Garman 1899

2. Head large, more than (40.5 − .03 L), sphenotic width of skull more than (17 − .015 L) per cent of L. Diameter of orbit more than (16.5 − .03 L) per cent of L. Articulation of lower jaw below the posterior one-third of orbit. Anterior supramaxillary extends forward beyond posterior supramaxillary by one-fourth of its length, or more.
   a. Head about (41 − .03 L), sphenotic width of skull less than (17.5 − .015 L) per cent of L. Interorbital width of skull less than (7.5 + .15 L) per cent of orbit. Posterior supramaxillary extends forward somewhat beyond the end of the anterior one-third of the anterior supramaxillary. Indo-Pacific. . . . . *B. macrolepis* Günther 1887
   b. Head more than (41.5 − .03 L) to (44 − .03 L) per cent of L. Sphenotic width of skull more than (17.5 − .015 L) per cent of L. Interorbital width of skull more than (7.5 + .15 L) to (25 + .15 L) per cent of orbit. Posterior supramaxillary barely reaches to, or slightly beyond the middle of anterior supramaxillary. Premaxillaries with upper, exterior row of horizontal, semi-elliptic platelike teeth. Atlantic. . . *B. koefoedi,* Parr 1951.

BIBLIOGRAPHY

Alcock, A.

1892. Natural history notes from the . . . "Investigator." Ann. Mag. Nat. Hist., ser. 6, vol. 10, no. 59, pp. 357–362.

Barnard, K. H.

1923. Diagnoses of new species of marine fishes from South African waters. Ann. So. Afr. Mus., Cape Town, vol. 13, pp. 439–444.

Beebe, W.

1929. Deep sea fish of the Hudson Gorge. Zoologica, New York, vol. 12, pp. 1–19.

Fowler, H. W.

1934. Descriptions of new fishes obtained 1907 to 1910 chiefly in the Philippine Islands and adjacent seas. Proc. Acad. Nat. Sci., Philadelphia, vol. 85, pp. 233–367.

Garman, S.

1899. Reports on an exploration . . . by the . . . "Albatross," during 1891. Mem. Mus. Comp. Zool., Harvard Coll., vol. 24, pp. 1–431.

Gilbert, C. H.

1891. Scientific results of explorations by the . . . "Albatross." Proc. U. S. Nat. Mus., vol. 14, pp. 545–546.

Gill, T.

1883. Diagnosis of new genera and species of deep-sea fish-like vertebrates. Proc. U. S. Nat. Mus., vol. 6, p. 256.

Goode, G. B., and T. H. Bean

1879. Description of *Alepocephalus bairdii.* Proc. U. S. Nat. Mus., vol. 2, p. 55.

Günther, A.

1878. Preliminary notices of deep-sea fishes collected during the voyage of H.M.S. "Challenger." Ann. Mag. Nat. Hist., ser. 5, vol. 2, pp. 248–251.

1887. Report on the deep-sea fishes collected by H.M.S. "Challenger" during the years 1873–76. Challenger Report, vol. 22, pt. 57, pp. 1–268.

Jordan, D. S., and W. F. Thompson

1914. Record of fishes obtained in Japan in 1911. Mem. Carnegie Mus., Pittsburgh, vol. 6, pp. 205–313.

Koefoed, E.

1927. Fishes from the sea-bottom. Rept. Sci. Res. "Michael Sars" N. Atlantic Exped. 1910, vol. 4, pt. 1, pp. 1–147.

Lloyd, R. E.

1909–10. A description of the deep-sea fish caught by R.I.M.S. ship "Investigator" since the year 1900. Mem. Indian Mus., vol. 2, pp. 139–180.

Norman, J. R.

1930. Oceanic fishes and flatfishes collected in 1925–1927. Discovery Report, vol. 2, pp. 261–370.

1939. Fishes. Sci. Rept. John Murray Exped., London, vol. 7, no. 1, pp. 1–116.

Parr, A. E.

1949. An approximate formula for stating taxonomically significant proportions of fishes with reference to growth changes. Copeia, 1949, no. 1, pp. 47–55.

1951. Preliminary revision of the Alepocephalidae, with the introduction of a new family, Searsidae. Amer. Mus. Novitates, no. 1531, pp. 1–21.

Risso, A.

1820. Memoire sur un nouveau genre de poisson. Mem. Ac. Sci. Nat. Torino, vol. 25, pp. 270–272.

Tanaka, S.

1908. Notes on some Japanese fishes. Jour. Coll. Sci. Tokyo, vol. 23, art. 7, pp. 1–54.

Townsend, C. H., and J. T. Nichols

1925. Deep sea fishes of the "Albatross" Lower California expedition. Bull. Amer. Mus. Nat. Hist., vol. 52, pp. 1–20.

Weber, M.

1913. Die Fische der Siboga Expedition. Siboga Expeditie. Leyden. pp. 1–710.

Zugmayer, E.

1911a. Diagnoses des poissons nouveaux provenant des campagnes du yacht "Princesse Alice." Bull. Inst. Oceanogr. Monaco, no. 193, pp. 1–14.

1911b. Poissons provenant des campagnes. Res. Camp. Sci. Monaco. fasc. 35, pp. 1–159.

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GEOGRAPHIC VARIATION IN THE RED-EYED TOWHEE OF THE EASTERN UNITED STATES

By J. C. Dickinson, Jr.

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM

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No. 5 — *Geographic Variation in the Red-eyed Towhee of the Eastern United States*[1]

J. C. Dickinson, Jr.
University of Florida

TABLE OF CONTENTS

Page
Introduction 274
Materials and Methods 274
Historical Summary 278
Status of Proposed Names 279
  Fringilla erythrophthalma Linnaeus 279
  Pipilo ater Vieillot 279
  Pipilo alleni Coues 280
  Pipilo leucopis Maynard 280
  Pipilo erythrophthalmus canaster Howell 280
  Pipilo erythrophthalmus leptoleucus Oberholser 280
  Pipilo alleni rileyi Koelz 283
The Subspecies of *Pipilo erythrophthalmus* 282
  Criteria Utilized 282
  Keys to Subspecies 284
  Pipilo erythrophthalmus erythrophthalmus Linnaeus 285
  Pipilo erythrophthalmus alleni Coues 292
  Pipilo erythrophthalmus canaster Howell 295
  Pipilo erythrophthalmus rileyi Koelz 299
Geographic Variation 304
  Wing Length 304
  Tail Length 312
  Tail Spot 313
  Culmen Length 315
  Width of Lower Mandible 317
  Tarsus Length 320
  Middle Toe without Claw 321
  Tail Spot: Tail 323
  Number of Rectrices Showing White on the Inner Web 324
  Iris Color 325
  Plumage Characteristics of Females 327
  Plumage Characteristics of Males 329
Non-Geographic Variation 330
Migratory Behavior 332
Variation in Relation to Environment 334
  Ecological Rules 334

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[1] Manuscript received for publication February 5, 1952.

Biotic Areas 336
Temperature Zones 336
Historical Factors 337
Summary 342
Acknowledgments 342
Literature Cited 344
Maps 349

INTRODUCTION

Previous investigations of geographical variation in the species *Pipilo erythrophthalmus* have been carried out by several individuals. For the most part these workers have considered only certain segments of a species of wide distribution in North America. Ranging from the Transition and Upper Austral zones east of the Great Plains from southeastern Saskatchewan, southern Manitoba, southern Ontario and southern Maine, south to central Texas, the gulf coast and peninsular Florida, the Red-eyed Towhee is subject to a variety of environmental conditions.

As a result of these earlier works, seven names have been proposed for use in designation of geographic races within the species. The present investigation was undertaken to determine the validity of these names, to determine the validity of the five races for which the names were proposed, to delimit the ranges of those races deemed valid, to gain additional knowledge of geographical variation within the species and within the various subspecies, and to add to the present store of information concerning the migratory behavior of the several populations. It was hoped that these lines of investigation might also shed some light on the reasons for the geographical variations observed.

MATERIALS AND METHODS

As true of most early workers in ornithology the pioneers in dealing with this species were forced to rely on small samples of populations which have wide geographic ranges. In the hope that the statistical analysis of larger series might prove enlightening a total of approximately 2300 specimens was assembled from various museums and private collections. The sources of these specimens, the number of specimens examined, the abbreviation for the collection used in the body of this report, and the persons to whom I am deeply indebted for arranging the loans are listed here.

American Museum of Natural History, 538 (AMNH) through J. T. Zimmer; Chicago Natural History Museum, 158 (CNHM) through E. R. Blake; Florida State Museum, 24 (FSM) through Nile C.

Schaffer; University of Georgia, Department of Zoology, 84 (DZUG) through E. P. Odum; Louisiana State Museum, at Louisiana State University, 106 (LSU) through George Lowery; Museum of Comparative Zoology at Harvard College, 131 (MCZ) through J. L. Peters; Carnegie Museum, 114 (CM) through W. E. C. Todd; United States National Museum including the collections of the Biological Survey, 770 (USNM) through A. Wetmore and A. J. Duval; University of Michigan Museum of Zoology, 83 (UMMZ) and the Max M. Peet collection at this same institution, 45 (MMP) through J. Van Tyne; North Carolina State Museum, 7 (NCS) through F. S. Barkalow, Jr.; Department of Biology, University of Florida, 6 (DBUF); private collections of Pierce Brodkorb, 7 (PB); G. M. Sutton, 17 (GMS) and Gideon Nelson, 6 (GN). Fifty-nine specimens in the Charleston Museum (CHAM) were not available on loan and they were studied in that museum through the kindness of E. Milby Burton, Director.

My own collections (JCD) from Gainesville and vicinity were augmented by field trips to various localities. April 17, 18, and 19, 1947, were spent on Dog and St. George Islands, Franklin County, Florida. July 22–27, 1947, was spent in southern Florida, Dade, Broward, Palm Beach, Martin and Monroe Counties. April 14–17, 1949, was spent in peninsular Florida, Hillsborough, Manatee, Sarasota, Broward, Charlotte, Polk and Martin Counties. April 20, 1949, was spent near Brunswick, Glynn County, Georgia, securing topotypical material and July 7–10, 1949, was spent in a trip to Mobile, Mobile County, Alabama, and the intervening territory in the panhandle of western Florida. These efforts contributed 83 specimens which are now deposited in the collection of the Museum of Comparative Zoology at Harvard College.

The following information was recorded from the museum label: museum number, locality, collector, date of collection, iris color, and any notation which the collector may have made in regard to condition of gonads and so forth. The condition of plumage with respect to amount of wear was judged subjectively and arbitrarily noted as fresh, slightly worn, worn, or very worn. Badly frayed specimens were excluded from consideration in examining the material in connection with wing length and tail length. The number of pairs of rectrices showing white on the innermost web was recorded. Individual variations in plumage color were noted — albinism, white tipping of the secondary coverts, abnormal color pattern of the contour feathers, and so forth.

The age of male specimens was judged on the basis of difference in color between the pale unmolted primary coverts and the darker secondaries in birds of the year. According to Dwight (1900) this difference in color does not occur in older birds. There appeared to be no difference in measurements in these two classes, and in the final analyses of data all specimens which had undergone the postjuvenal molt were utilized.

Iris color of specimens collected by other persons was for the most part lacking. When notation of color was made, in many instances it was extremely difficult to use. It is worthwhile to point out some of the specific difficulties encountered in that many of them could be avoided by proper techniques on the part of collectors in the future. Many, certainly the majority of the specimens lacked any notation as to iris color at all. A great variety of words and phrases were used to describe the color, such as straw, buff, orange, yellow tinged with red, red tinged with yellow, salmon, brownish, red brown, light, scarlet, deep red, like the flanks, same as female No. 0000 (but no such female in the material at hand), almost like the Florida bird, light red, clear yellow, white, yellowish white. These represent a sampling of some of the designations used. It is apparent that there has been a tendency on the part of collectors to record iris color if they thought that it was unusual to have a particular color in the locality from which the specimen was taken. If the color present was thought to be the usual one in that particular locality then no notation was made. This presents certain difficulties. What did the collector assume to be the normal color and on what basis? Did he single out this bird in the field and collect it because of its unusual iris? As a result it is very difficult to visualize true conditions with respect to this important geographically varying character.

Iris color on material taken personally was, in so far as possible, noted in terms of the color charts published by Maerz and Paul (1930). In addition, if it was practical to bring the birds in the flesh to the University of Florida, Miss E. Coogle, Staff Artist in the Department of Biology, recorded iris color on the label with matching water colors. At this time comparison was made with Maerz and Paul and the color match noted on the label.

Measurements were all recorded in millimeters after having been made as described below.

Wing length. Measured flat with right angle rule against bend of folded wing, and feathers pressed to fullest extent, to end of longest primary.

Tail length. Measured with dividers, one point of which was inserted between the shafts of the middle pair of rectrices at the base and pressed forward as far as it would go, the other touching the extremity of the longest rectrix.

Culmen. Measured with dividers from the base to the tip of the upper mandible.

Depth of bill. Measured with vernier calipers, one arm on highest portion of culmen, the other across the lower edge of the mandibular rami at the end of the rhamphotheca.

Width of lower mandible. Measured with vernier calipers, across the chin, at the widest point of the rhamphotheca.

Tarsus. Measured with dividers, from the tibio-tarsal joint on the outer side to the lower end.

Middle toe. Measured with dividers, from the lower end of the tarsus to the base of the claw.

Tail spot. Measured with vernier calipers, one arm at upper limit of white on inner web of outermost rectrix, the other touching the end of the feather.

Wing spot. Measured with vernier calipers, one arm at the distal end of the primary coverts, the other at the greatest extent of white on the primaries.

Depth of bill was not utilized in arriving at conclusions presented here. It appeared that the technique of measurement for this character as outlined above was not reliable. Specimens measured twice did not produce the same results within limits of what might be considered reasonable. Individual techniques as practiced by various collectors seemed to materially influence the results obtained in measuring. Wing spot was also eliminated in that no proper technique was found for producing accurate measurements of this character.

Data were recorded on standard 5 x 8 inch McBee Keysort cards. It was hoped that these cards would serve in such a study as this, but the multiplicity of characters and variation of these characters precluded their use in the manner for which they were designed.

The specimen cards were sorted into many small samples, approximately 50, representing small geographic areas, and studied as fractional parts of the whole population to better visualize general trends in variation of the separate characters. In this material were included only those birds that were felt to be definitely breeding or resident individuals. The criterion used in this regard was arbitrarily the date of collection — May through August. Undoubtedly many individual breeding specimens were thus excluded, but it was felt that any bias encountered here was on the conservative side. Winter, or non-breeding specimens were considered as being those birds taken from November through February for the northern areas, and October through April for the Florida material. September-October and March-April specimens were considered as possibly being on migration and were excluded for this reason.

At the conclusion of the collection of data standard statistical methods of analysis were used as outlined by Simpson and Roe (1939, 1942), and Cazier and Bacon (1949).

HISTORICAL SUMMARY

Of the seven names proposed for use in dealing with the various populations of *Pipilo erythrophthalmus* Linnaeus, *Passer niger, oculis rubris,* (Catesby, 1731: 34, pl. 34) furnishes a point of departure. Catesby described the "towhee-bird" on the basis of birds seen, and presumably taken, in South Carolina. Linnaeus (1758: 180) proposed the name *Fringilla erythrophthalma* for Catesby's bird. Vieillot (1819: 292) placed it in the genus *Pipilo* which he had erected (1816: 32) and proposed a new name *Pipilo ater* for use in designating this species.

Elliot Coues (1871: 366, footnote) recognized a new form from measurements of specimens taken at Dummitts, Florida, by C. J. Maynard, and published by Allen (1871: 283). He suggested the name *Pipilo alleni* for this form.

Maynard (1878: 113, pl. 4) later proposed *Pipilo leucopis* for this same form. Shortly thereafter he (Maynard, 1881: iv) indicated that he felt that Coues had, though perhaps inadvertently, usurped a prerogative of his in taking this action.

A. H. Howell (1913: 202) proposed a fifth name, *Pipilo erythrophthalmus canaster,* for a form occurring at Spring Hill, Alabama.

H. C. Oberholser (1938: 641) stated that the birds of New Orleans and vicinity were sufficiently different from the remainder of the population to be worthy of subspecific rank and designated these birds as *Pipilo erythrophthalmus leptoleucus.*

Walter Koelz (1939: 121) proposed the seventh available name, *Pipilo alleni rileyi,* for use in designating the birds found at Brunswick, Georgia, which he felt were different from the Florida form.

Action by the American Ornithologists' Union to date (1886, 1895, 1910, 1931 and various supplements) has accorded recognition to *Pipilo erythrophthalmus erythrophthalmus* (Linn.), *Pipilo erythrophthalmus canaster* Howell and *Pipilo erythrophthalmus alleni* Coues. The type locality of *P. e. erythrophthalmus* has been designated as South Carolina by this same group.

Much attention has been paid to geographic variation in the species, and efforts were made on the part of the original describers and by others to come to conclusions as to the geographic range of the various forms. Howell (1932: 449) amended his original statements in connection with *P. e. canaster* by noting that iris color, instead of being red throughout the range of this subspecies, was variable — red, reddish or straw color. He also added notes on range to indicate that this form occupied most of Alabama, Georgia, northwestern Florida, and southern Mississippi and extended east to the coast of South Carolina. Koelz (1939: 122) suggested that the pale-eyed Florida and Georgia birds were sufficiently different from the dark-eyed birds of the north to be worthy of specific rank. By listing paratypes, from localities which he apparently felt were within the limits of geographic range, he outlined the extent of this population. Burleigh (1937: 459; 1944: 473–474) commented on the occurrence of the various races in the coastal areas of North Carolina and Mississippi. Worthington and Todd (1926: 219) contributed critical notes on the occurrence of intermediate specimens during the winter at Choctawhatchee Bay, Florida. Pearson, Brimley and Brimley (1942: 235) quoted pertinent correspondence from Alexander Wetmore concerning the distribution of *P. e. canaster, alleni* and *erythrophthalmus* in North Carolina. Ridgway (1901: 424) commented on east-west variation in *P. e. erythrophthalmus*. Oberholser (1938: 642–644) gave much information concerning the distribution of the Louisiana population for which he proposed the name *P. e. leptoleucus*. The range was indicated as including southeastern and central Louisiana. Birds from Baton Rouge and northward were referred to as *P. e. canaster*. Wetmore (1937a, b), Murphey (1937: 58), Howell (1928: 248–249), Allen (1871, 1872 and 1878), Ridgway (1901: 423–427) and Maynard (1881: 113) contributed much to the present knowledge of the species with comments on range, variation, measurements, migratory behavior, ecology, etc.

STATUS OF PROPOSED NAMES

FRINGILLA ERYTHROPHTHALMA Linnaeus

The status of this name after its proper placement in the genus *Pipilo* by Vieillot in 1819 is involved with that of *Pipilo erythrophthalmus canaster* Howell and is discussed under that heading.

PIPILO ATER Vieillot

Vieillot proposed this name in 1819, to replace *Emberiza erythrophthalma* Latham. He also quotes Catesby and Wilson in his remarks. Since *Emberiza erythrophthalma* Latham is a synonym of *Fringilla erythrophthalma* Linn., *Pipilo ater* must also be a synonym of Linnaeus' name.

PIPILO ALLENI Coues vs. PIPILO LEUCOPIS Maynard

Despite the fact that Coues' action interfered with Maynard's intention of describing this form, *Pipilo alleni* Coues has priority over *Pipilo leucopis*. The original thought on the part of both Maynard and Coues as to the specific distinctness of this form has of course been shown in modern times to be fallacious, and its true status as a geographic race of *P. erythrophthalmus* is obvious.

PIPILO ERYTHROPHTHALMUS CANASTER Howell

Howell was certainly correct when he proposed that the Alabama birds were different from the form occurring in the northern part of the United States. It is unfortunate, however, that he did not investigate the status of the birds from the type locality of *P. e. erythrophthalmus*. Catesby (1731) may have had *P. e. canaster* at hand when he originally described the South Carolina form as *Passer niger, oculis rubris*. There are of course no Catesbian specimens available but the wording of the discussion of habits is such as to indicate that he was referring to the resident form occurring in South Carolina. Statements such as "a solitary bird," "one seldom sees them but in pairs," "they breed and abide all the year in Carolina in the shadiest woods," would indicate that he was aware of the summer conditions in this area. It is known that he made a trip up the Savannah River as far as Richmond County, Georgia. The greater portion of the geographic area of South Carolina has *canaster* as its breeding race today, and there is no indication that this condition has come about since the time of Catesby. Additionally, the included map in Catesby (1731) indicates that "Carolina" was taken to include a considerable area outside the present political boundaries of South Carolina. Despite this evidence I do not feel that it is worthwhile to re-arrange the names in this species at this time for the following reasons:

(1) Howell, the first reviser, chose to restrict Linnaeus' name to the northern population.

(2) The resultant confusion in the old literature coming about as the result of the change would outweigh the advantage of precise accuracy from a historical standpoint. Therefore I feel that it is preferable to retain the current usage of these names.

PIPILO ERYTHROPHTHALMUS LEPTOLEUCUS Oberholser

This name, proposed by Oberholser for the towhees of New Orleans and vicinity, must be placed in synonymy with *P. e. canaster* Howell.

Fifteen topotypical males from Orleans Parish were available and they provide the following mean measurements with their standard errors: wing, 87.57 ± .81; tail, 93.29 ± .72; tail spot, 30.79 ± 1.19; culmen, 15.39 ± .09; width of lower mandible, 8.88 ± .06; tarsus, 27.67 ± .27; middle toe, 20.23 ± .21 mm. These means are not significantly different[1] from those found for *P. e. canaster,* and each of the specimens conforms in all measurements to the limits of variation of the latter. A single female was available and it is typical of *canaster*. Specimens examined in this connection are listed with those appearing under *P. e. canaster,* from Orleans Parish. Two of these, USNM 341594 and 363222, were apparently among those examined by Oberholser. Two others, USNM 340500 and LSU 1626 from St. Bernard and Assumption Parishes, respectively, are also mentioned by Oberholser as being referable to this race. I find that they are typical of *P. e. canaster.*

PIPILO ALLENI RILEYI Koelz

In his original description Koelz stated that the red-eyed and pale-eyed forms were specifically distinct. He felt that this name should be applied to a population which was not a part of the red-eyed species occurring to the northward but rather a portion of the peninsular Florida form. His position in this may be well taken if means are discovered to allow a nomenclatorial differentiation of re-united populations as opposed to populations which are in the process of becoming distinct. It is certainly possible that the pale-eyed stock was at one time isolated from the continental population, although this situation no longer exists. There is no question that intergradation occurs between all adjacent forms. The characters involved in this situation, iris color, wing length, tail spot, etc., all show blending. At present there does not appear to be evidence to allow specific recognition of the pale-eyed forms, *alleni* and *rileyi*. Miller (1949: 338) discusses the problem of distinguishing between hybridization and intergradation. He concludes that hybridization implies lack of blended inheritance and that intergradation should be taken to indicate a blending of characters. Present day knowledge of genetic principles does not lend support to this suggestion.

Koelz was correct in his estimate of the validity of differences between the peninsular Florida population and the pale-eyed form occurring along the coast of North and South Carolina and in southeast Georgia. This form should be designated as *Pipilo erythrophthalmus rileyi* Koelz.

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[1] These means fall within one standard error of the means of *P. e. canaster* except tarsus which falls within two standard errors.

THE SUBSPECIES OF PIPILO ERYTHROPHTHALMUS

Criteria Utilized

Much debate has gone on in regard to the proper rules and regulations which should be adopted by taxonomists in their recognition of subspecies. Most workers seem to agree that the subspecies level is certainly a subjective one, and yet much effort has been expended in an effort to reduce this problem to terms of objective criteria.

The advent of statistical study has of course been of much assistance in allowing the taxonomist to better estimate what might well be called the population phenotype from a relatively small sample of a population. It has also made it possible to better visualize the differences that exist between two or more populations. It seems that in addition to these benefits, however, statistical analysis leads the taxonomist into the feeling that the final equations will furnish an exact and clear answer to his problems. Indeed, on some occasions the statistics become the "end" rather than the "means." The fallacy is obvious — the units that are being dealt with are not numbers but rather simply measures of various expressions of certain genotypes and environments. The specimens concerned must be viewed as live animals, and the whole problem must remain in reality a biological one.

In ornithological studies in large part the taxonomist is dealing with continuous variates and with variation that appears graphically as a cline. Under such circumstances lines of demarcation between variant populations of necessity must be vague. There most certainly will be large portions of the populations that are not clearly identifiable.

Rand and Traylor (1950: 174) in their review of this problem conclude that five principal criteria of separability are in common use today:

1. The average of one subspecies separable from the average of the other subspecies.
2. 75 per cent of one separable from all of the other.
3. 50 per cent of one separable from all of the other.
4. 75 per cent of one separable from 75 per cent of the other.
5. The means of the two forms separable by the sum of their standard deviations (= 84 per cent from 84 per cent).

Amadon (1949), in summation of his discussion of this problem, adds to these "97 per cent from 97 per cent," which he recommends for adoption.

Rand and Traylor seem to lack the courage of their convictions (or the convictions themselves). They make a rather vague suggestion as to the degree of separability which should be demanded, *i.e.* about

80 to 90 per cent of one race separable from about 80 to 90 per cent of the other. They further fail to indicate whether this criterion of separation should be applied to statistical estimates of variability of the races or to particular samples at hand. From the examples given, unfortunately, it appears that the latter is the method used. In many cases this method may give a faulty impression of the limits of variability.

The problems that immediately arise in either case are manifold. Does the sample really represent the population? How large a geographic area may be visualized as the range of the races as opposed to the area of intergradation between the two? How large is the sample at hand? Is any subjective or mechanical bias present? Will naming the populations serve any useful purpose?

These problems are subjective ones and certainly no mathematical formulae will solve them. Under the circumstances it does not seem practical to try to establish any set degree of separability as the criterion for nomenclatorial recognition. In some cases if other factors, such as geographic area, are included, 50 per cent from 50 per cent separation might serve and in others 100 per cent from 100 per cent might not. Races must be visualized as transitory phenomena in the evolutionary development of the organism. The status of the populations as they are examined on the basis of contemporary specimens cannot be looked upon as a static situation. Existing environmental conditions may change, attended by morphological changes in the organism.

Another factor which must be considered, but which for the most part has been omitted from consideration, is the individual taxonomist's desire to name something. There seems to be little reason for doubting that this factor on many occasions has entered the picture, and there is reason to assume that the taxonomist is on some occasions biased in his conclusions by this factor.

It appears that in proposing criteria to be used in designation of subspecies the following should be paramount. Does naming the population serve any useful purpose? For example, is it possible in the case of migratory species to identify the breeding area of a winter-taken specimen? Is it possible to identify correctly a major portion of the population, not only in terms of "per cent from per cent," but in terms of area inhabited by identifiable populations versus area of intergradation? Is a clearer picture of relationships presented by furnishing the populations with names? In that these are subjective decisions it does not seem practical to follow Amadon in proposing an iron-clad degree of separability as the criterion. Some leeway must be observed in this respect, otherwise the whole structure of taxonomy will suffer. Rand and Traylor's suggestion of about 80 to 90 per cent separability, if modified to about 80 per cent, may well be the most practical minimum — if the other subjective criteria mentioned are included.

In arriving at the conclusions presented here, following statistical analyses of variability, 75 per cent from 75 per cent has been the criterion of separability utilized. Other considerations, however, have been included. This is evidenced by my declining to name the eastern and western segments of the population designated as *P. e. erythrophthalmus,* despite the fact that in males, 74.5 per cent separation is obtained on the basis of tail and length of wing.[1] In this case the fact that a major portion of the range of the form here designated as *erythrophthalmus* would be inhabited by intermediate, unidentifiable birds seems to overrule the desirability of such action (Map 1). In the four subspecies recognized a minimum of 75 per cent separability obtains, and in addition the areas of intergradation are small (Map 2). There is also correlation of morphological variation with environmental and physiographic differences, and a reasonable phylogenetic picture may be visualized.

Keys to Subspecies

In the keys which follow, the index characters are listed in the order of diminishing degree of separation. In all cases the first character mentioned in each couplet furnishes at least 75 per cent separation.

Iris color of birds in first winter plumage presents certain difficulty in the use of these keys, since the iris may not yet have taken on the adult appearance. As mentioned in another connection in this report, *alleni* and *rileyi* both have grayish irides at this time, whereas *erythrophthalmus* and *canaster* have brownish irides.

Adult Males

1. Wing usually less than 83.0 mm., tail spot usually less than 23.0 mm., tarsus usually less than 27.5 mm., middle toe usually less than 19.5 mm., iris straw colored . . . . *alleni*

1a. Wing usually 83.0 mm. or more, tail spot usually 23.0 mm. or more, tarsus usually 27.5 mm. or more, middle toe usually 19.5 mm. or more, iris variable in color 2

2. Iris usually straw, buff or yellow (sometimes orange), tail spot usually less than 28.2 mm. (usually more than 23.0 mm.) . . . . *rileyi*

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[1] This degree of separability is inversely related to geographic area — the larger the area, the less separability. It reaches its maximum when samples from widely separated localities are compared. For example, 84 per cent of North Dakota, Iowa, Minnesota and Wisconsin were separable from a series taken on Long Island, New York.

2a. Iris variable but usually red, tail spot usually 28.2 mm. or more.......3
3. Culmen usually less than 15.0 mm., tail spot/tail ratio usually 36.0 per cent or more, iris red............................*erythrophthalmus*
3a. Culmen usually 15.0 mm. or more, tail spot/tail ratio usually less than 36.0 per cent, iris usually red but sometimes orange, buff or yellow..*canaster*

Adult Females

1. Tail spot usually less than 19.5 mm., wing usually less than 78.0 mm., iris straw..*alleni*
1a. Tail spot usually 19.5 mm. or more, wing usually 78.0 mm. or more, iris variable..2
2. Iris usually straw, buff or yellow (sometimes orange), wing usually 82.1 mm. or less (more than 78.0 mm.), tail spot usually less than 24.6 mm...*rileyi*
2a. Iris usually red (sometimes orange, buff or yellow), wing usually 82.2 mm. or more, tail spot usually 24.6 mm. or more......................3
3. Tail spot/tail ratio usually 30.3 per cent or more, tail spot usually 28.7 mm. or more, culmen usually 14.8 mm. or less, tarsus 27.2 mm. or more, iris red.....................................*erythrophthalmus*
3a. Tail spot/tail ratio usually less than 30.3 per cent, tail spot usually less than 28.7 mm., culmen usually more than 14.8 mm., tarsus usually less than 27.2 mm., iris usually red but sometimes orange, buff or yellow..*canaster*

PIPILO ERYTHROPHTHALMUS ERYTHROPHTHALMUS Linnaeus

Fringilla erythrophthalmus Linnaeus (1758: 180), description based on Catesby (Vol. 1: 34, pl. 34). Type locality: South Carolina.
Pipilo ater Vieillot (1819: 292).
Pipillo erythrophthalmus, Vieillot (1824: 109, pl. 80).
Pipilo erythrophthalmus var. *erythrophthalmus*, Baird, Brewer, and Ridgway (1874: 108).

Description

Diagnosis. A large, small-billed, vividly colored, red-eyed form, showing a large amount of white on the rectrices.

Average dimensions of males. Wing, 87.57 ± .15 (σ, 2.77); tail, 92.91 ± .20 (σ, 3.82); culmen, 14.49 ± .03 (σ, 0.58); width of lower mandible, 8.68 ± .02 (σ, 0.29); tarsus, 27.37 ± .05 (σ, 0.90); middle toe without claw, 19.64 ± .04 (σ, 0.71); length of white on inner web of outermost rectrix, 36.70 ± .24 (σ, 4.47); tail spot/tail ratio, 39.36 ± .27 (σ, 4.96). (See Table 1.)

Average dimensions of females. Wing, 83.38 ± .28 (σ, 2.68); tail, 88.22 ± .41 (σ, 3.80); culmen, 14.47 ± .62 (σ, 0.07); width of lower mandible, 8.60 ± .04 (σ, 0.33); tarsus, 26.60 ± .10 (σ, 0.96); middle toe without claw, 19.06 ± .07 (σ, 0.71); length of white on inner web of outermost rectrix, 33.18 ± .46 (σ, 4.29); tail spot/tail ratio, 37.47 ±.51 (σ, 4.67). (See Table 2.)

Table 1
P. e. erythrophthalmus
Males

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	359	87.57	.15	2.77	84.81–90.34	80.0– 96.0
Tail	351	92.91	.20	3.82	89.09–96.73	82.0–104.0
Tail Spot	345	36.70	.24	4.47	32.23–41.17	23.6– 55.0
Culmen	350	14.49	.03	.58	13.92–15.07	13.1– 16.0
Mandible Width	346	8.68	.02	.29	8.39– 8.97	7.5– 9.5
Tarsus	355	27.37	.05	.90	26.48–28.27	24.8– 29.5
Middle Toe	351	19.64	.04	.71	18.93–20.35	17.4– 22.4
Tail Spot/Tail	340	39.36	.27	4.96	34.40–44.32	26.0– 61.0

Table 2
P. e. erythrophthalmus
Females

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	95	83.38	.28	2.68	80.70–86.06	77.0–89.5
Tail	90	88.22	.41	3.80	84.42–92.03	78.0–96.5
Tail Spot	90	33.18	.46	4.29	28.90–37.47	24.6–45.3
Culmen	91	14.47	.07	.62	13.85–15.09	13.0–15.4
Mandible Width	90	8.60	.04	.33	8.27– 8.94	7.8– 9.4
Tarsus	90	26.60	.10	.96	25.64–27.57	24.0–29.0
Middle Toe	92	19.06	.07	.71	18.36–19.77	17.0–20.4
Tail Spot/Tail	85	37.47	.51	4.67	32.81–42.14	28.0–55.0

Average color of males.[1] Back, Sooty Black; flanks, 5-D-12; breast, Sooty Black; top of head, Sooty Black.

Average color of females. Back, 15-J-8; flanks, 13-H-12; breast, 14-K-9; top of head, 8-L-12.

Iris Color. Red.

Breeding range. Transition and Upper Austral zones east of the Great Plains from southern Saskatchewan, southern Manitoba, southern Ontario and southern Maine, south through middle North Dakota, Iowa, Kansas and northern Arkansas, east through middle Tennessee and northern Georgia and western South Carolina to the Atlantic coast in southern Virginia (Princess Anne County). Casual in New Brunswick. (See Map 2.)

Winter range. From southeast Texas, Louisiana, Mississippi, Tennessee and North Carolina south to the Gulf Coast and mid-peninsular Florida. Occasionally as far north as southeastern Nebraska, Iowa, Wisconsin, Illinois, southern Michigan, Ohio, Pennsylvania, southern New York and Massachusetts. (See Map 3.)

Comments. During the winter months this towhee moves south into the ranges of the other three races, extending well down into peninsular Florida in the east and into east Texas in the west. During this season it is prone to congregate in flocks of 10–15 individuals and is often seen in company with the resident form of the locality in which it is spending the winter. When in Florida *P. e. erythrophthalmus* prefers much heavier cover than does *P. e. alleni* and it is most regularly seen along the edges of fairly dense hardwood hammocks. It does not appear to be unusual for some individuals to remain in the breeding area during the winter. Numerous published records attest to this, and in the material examined by me seven individuals were taken in the north during the winter months.

Specimens Examined

Atypical specimens are indicated as follows:
**erythrophthalmus* > *canaster*
***erythrophthalmus* > *rileyi*

Breeding Males.[2] ARKANSAS: Washington Co., 4 (AMNH). CONNECTICUT: Fairfield Co., 3 (AMNH); New Haven Co., 2 (AMNH). GEORGIA: Fannin Co., 1 (MMP), 2 (USNM); Habersham Co., 1 (USNM); Rabun Co., 4 (USNM), 1 (LSU); Townes Co.,

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[1] For explanation of color nomenclature see discussion on p. 329.

[2] Breeding material includes all those individuals utilized in arriving at the estimates of the characters of the population. For this reason some atypical specimens are included under this heading.

1*(USNM); Union Co., 1*(MMP), 2 (USNM); White Co., 1 (USNM). ILLINOIS: Cook Co., 4 (CNHM); Fulton Co., 1 (CNHM); Lake Co., 1 (AMNH); Marshall Co., 1 (CNHM); Pulaski Co., 4 (CNHM); Will Co., 7 (CNHM). INDIANA: Knox Co., 1 (AMNH); Lake Co., 1 (CNHM); Marion Co., 1 (UMMZ); Wells Co., 2 (CNHM). IOWA: Linn Co., 1 (CNHM); Marion Co., 1 (AMNH). KENTUCKY: Madison Co., 1 (USNM); Union Co., 1 (USNM); Harlan Co., 1 (USNM). MARYLAND: Montgomery Co., 1 (CM); Prince George Co., 1 (AMNH). MASSACHUSETTS: Barnstable Co., 1 (AMNH); Hampshire Co., 1 (AMNH); Middlesex Co., 4 (AMNH); Norfolk Co., 1 (AMNH), 1 (USNM). MICHIGAN: Berrien Co., 1 (UMMZ); Calhoun Co., 1 (UMMZ); Charlevoix Co., 3 (UMMZ); Cheboygan Co., 1 (MMP); Chippewa Co., 1 (UMMZ); Huron Co., 1 (UMMZ); Ionia Co., 1 (AMNH); Kalamazoo Co., 2 (UMMZ); Livingston Co., 3 (UMMZ); Menominee Co., 1 (UMMZ); Oscoda Co., 1 (UMMZ); Washtenaw Co., 4 (MMP), 3 (GMS), 3 (UMMZ); Wexford Co., 1 (AMNH). MINNESOTA: Hennepin Co., 1 (AMNH); Olmstead Co., 2 (AMNH). MISSOURI: Wayne Co., 1 (USNM). NEW HAMPSHIRE: Hillsboro Co., 1 (AMNH). NEW JERSEY: Bergen Co., 4 (AMNH); Essex Co., 4 (AMNH); Mercer Co., 1 (AMNH); Middlesex Co., 1 (AMNH); Morris Co., 2 (AMNH); County Unknown, 2 (AMNH). NEW YORK: Erie Co., 1 (AMNH); Jefferson Co., 1 (AMNH); Kings Co., 3 (AMNH); Nassau Co., 1 (MMP), 7 (AMNH); New York Co., 3 (AMNH); Orange Co., 1 (AMNH), 4 (USNM); Putnam Co., 1 (AMNH); Queens Co., 15 (AMNH); Rensselaer Co,. 1 (AMNH); Richmond Co., 1 (AMNH); Rockland Co., 3 (AMNH); Suffolk Co., 1 (CM), 1 (UMMZ), 52 (AMNH); Westchester Co., 6 (AMNH). NORTH CAROLINA: Buncombe Co., 5 (USNM); Burke Co., 1 (USNM); Cherokee Co., 1* (USNM); Greenville Co., 1 (USNM); Jackson Co., 1 (MCZ); Macon Co., 1* (USNM), 2 (USNM), 1* (DZUG), 6 (DZUG); Sampson Co., 1 (USNM); Transylvania Co., 2 (USNM); Watauga Co., 2 (USNM); Yancey Co., 1* (USNM), 2 (USNM). NORTH DAKOTA: Towner Co., 1 (CNHM), 6 (UMMZ). OHIO: Portage Co., 1 (AMNH). PENNSYLVANIA: Beaver Co., 7 (CM); Bedford Co., 1 (CM); Blair Co., 1 (AMNH); Butler Co., 1 (CM); Cambria Co., 1 (AMNH), 2 (CM); Columbia Co., 1 (CM); Crawford Co., 3 (CM); Erie Co., 2 (AMNH); Fayette Co., 1 (LSU); Pike Co., 1 (AMNH); Washington Co., 1 (CM). RHODE ISLAND: Providence Co., 4 (AMNH). SOUTH CAROLINA: Anderson Co., 1 (USNM); Cherokee Co., 1 (USNM); Greenville Co., 2 (CHAM), 1* (USNM), 1 (USNM), 1* (AMNH), 2 (AMNH); Pickens Co., 2* (USNM). TENNESSEE: Anderson Co., 1 (USNM); Campbell Co., 2 (UMMZ); Cocke Co., 1 (USNM); Cumberland Co., 1 (USNM); Johnson Co., 5 (USNM); Munroe Co., 1 (UMMZ); Sullivan Co., 1 (USNM); Van Buren Co., 1 (USNM). VIRGINIA: Accomac Co., 4* (USNM), 1 (USNM); Arlington Co., 1 (AMNH); Augusta Co., 3 (USNM); Fairfax Co., 1* (AMNH), 1 (AMNH); Highlands Co., 2 (USNM); Norfolk Co., 1 (LSU), 1* (USNM); Northampton Co., 2 (USNM); Princess Anne Co., 1* (UMMZ); Rockbridge Co., 5 (USNM); Smythe Co., 1 (USNM); Spotsylvania Co., 1 (USNM); Wythe Co., 4 (MCZ). VERMONT: Wyndham Co., 1 (AMNH). WASHINGTON, D. C.: 2 (CM). WEST VIRGINIA: Calhoun Co., 1 (USNM); Barbour Co., 1 (USNM); Brooke Co., 1 (MMP); Nicholas Co., 1 (USNM); Pendleton Co., 1 (MMP); Pocohontas Co., 2 (USNM); Randolph Co., 1 (USNM); Tucker Co., 1 (UMMZ), 1 (USNM). WISCONSIN: Burnett Co., 1 (USNM); Dodge Co., 7 (CNHM); Juneau Co., 2 (AMNH); Rock Co., 1 (FSM); Walworth Co., 3 (AMNH); ?Selinctous? 1 (CM).

Breeding females. CONNECTICUT: New Haven Co., 2 (AMNH). GEORGIA: Habersham Co., 1 (USNM); Rabun Co., 1 (USNM); Townes Co., 2 (USNM); White Co., 1* (USNM). KENTUCKY: Harlan Co., 1 (USNM); Union Co., 1 (USNM). MARYLAND: Montgomery Co., 5 (USNM); Prince George Co., 1 (AMNH). MASSACHUSETTS: Barnstable Co., 1 (AMNH); Middlesex Co., 1 (AMNH). MICHIGAN: Berrien Co., 1 (UMMZ); Charlevoix Co., 2 (UMMZ); Chippewa Co., 1 (UMMZ); Huron Co., 1 (UMMZ); Jackson Co., 2 (UMMZ); Kalamazoo Co., 1 (UMMZ); Lapeer Co., 1 (UMMZ); Leelanau Co., 1 (UMMZ); Washtenaw Co., 4 (MMP), 1 (GMS). NEW YORK: Kings Co., 1 (AMNH); Nassau Co., 2 (AMNH), 1 (USNM); Orange Co., 2 (AMNH); Queens Co., 2 (AMNH); Suffolk Co., 7 (AMNH), 1 (UMMZ). NORTH CAROLINA: Buncombe Co., 1 (LSU), 1 (USNM); Macon Co., 1 (MCZ); Sampson Co., 1 (USNM); Wake Co., 1 (NCS); Watauga Co., 1 (USNM). NORTH DAKOTA: Towner Co., 3 (UMMZ). PENNSYLVANIA: Beaver Co., 1 (CM); Cambria Co., 1 (CM); Crawford Co., 1 (CM); Westmorland Co., 2 (CM). SOUTH CAROLINA: Greenville Co., 2 (AMNH), 1 (CHAM), 1 (USNM). TENNESSEE: Cocke Co., 1 (USNM); Cumberland Co., 1* (USNM), 1 (USNM); Johnson Co., 1 (USNM). VIRGINIA: Accomac Co., 1 (USNM); Arlington Co., 1 (AMNH); Giles Co., 1 (AMNH), 2 (MCZ); Highlands Co., 2 (USNM); North Hampton Co., 1 (CM); Elliot Knob, 1 (USNM). WASHINGTON, D. C.: 1 (AMNH), 2 (CM), 1 (USNM). WEST VIRGINIA: Barbour Co., 1 (USNM); Ohio Co., 1 (MMP); Randolph Co., 1 (USNM); Tucker Co., 1 (AMNH), 1 (GMS); Zeld, 1 (USNM). WISCONSIN: Vilas Co., 1 (USNM); Walworth Co., 2 (AMNH).

Wintering Males.[1] ALABAMA: Autauga Co., 1 (USNM); Houston Co., 1* (USNM); Montgomery Co., 2 (USNM). ARKANSAS: Crawford Co., 1 (USNM). FLORIDA: Alachua Co., 1 (AMNH), 4 (FSM), 1 (JCD); Citrus Co., 1 (FSM); Duval Co., 2 (MCZ), 4 (USNM); Escambia Co., 2 (USNM); Leon Co., 1* (CNHM), 1 (CNHM); Levy Co., 1 (AMNH), 1 (MCZ), 1 (JCD); Nassau Co., 3 (AMNH); Okaloosa Co., 7 (CM); Okeechobee Co., 1 (USNM); Pinellas Co., 1 (MCZ); Polk Co., 1 (USNM); Putnam Co., 2 (USNM); 2 (CNHM); St. Johns Co., 2 (AMNH); Santa Rosa Co., 8 (CM); Wakulla Co., 2 (USNM), 1* (USNM), 2 (FSM), 1 (JCD). GEORGIA: Barrow Co., 1 (USNM); Bibb Co., 1 (USNM); Camden Co., 1 (MCZ); Catoosa Co., 1 (USNM); Charlton Co., 3 (USNM); Chatham Co., 2 (MCZ); 1 (USNM); Cherokee Co., 1 (USNM); Clarke Co., 8 (USNM), 1* (USNM); Cobb Co., 1 (CNHM); De Kalb Co., 5 (USNM), 2* (USNM); Early Co., 1 (USNM); Fulton Co., 6 (USNM); Glynn Co., 1(MCZ); Hall Co., 1 (USNM); Heard Co., 1 (USNM); McIntosh Co., 1 (AMNH); Thomas Co., 1 (AMNH), 1 (USNM). KENTUCKY: Butler Co., 1 (USNM). LOUISIANA: Cameron Parish, 1 (LSU); East Baton Rouge Parish, 2 (CNHM), 4 (LSU), 1* (LSU), 1 (USNM); Ouachita Parish, 1 (LSU); Orleans Parish, 1* (LSU), 2 (USNM); West Feliciana Parish, 2 (LSU). MARYLAND: Worcester Co., 1 (USNM). MISSISSIPPI: Bolivar Co., 1 (CNHM); Harrison Co., 6 (USNM), 4 (LSU); Warren Co., 2 (LSU). NEW JERSEY: Morris Co., 1 (AMNH). NORTH CAROLINA: Brunswick Co., 1 (NCS); Buncombe Co., 3 (USNM), 1 (MCZ); Carteret Co., 1 (USNM); Robeson Co., 1 (CNHM); Transylvania Co., 2 (USNM); Yancey Co., 1 (USNM). OHIO: Pickaway Co., 1 (AMNH). SOUTH CAROLINA: Beaufort Co., 2 (MCZ); Berkeley Co., 1 (CHAM); Charleston Co., 5 (CHAM), 1 (LSU), 1 (USNM); Horry Co., 1 (CHAM); Kershaw Co., 5 (USNM); Pickens Co., 1 (CHAM). TENNESSEE: Giles Co., 2 (USNM); Hamilton Co., 1 (USNM); Shelby Co., 3 (LSU). TEXAS: Lee Co., 1 (AMNH); Nueces Co., 1 (AMNH). WEST VIRGINIA: Brooke Co., 1 (GMS); Cabell Co., 1 (USNM).

Wintering females. ALABAMA: Autauga Co., 1 (USNM); Jackson Co., 1* (USNM); Ardell, 2 (USNM); Orange Beach, 1 (USNM). FLORIDA: Alachua Co., 2 (FSM), 1 (JCD); Duval Co., 1 (MCZ); Levy Co., 1* (MCZ); Okaloosa Co., 5 (CM); Okechobee Co., 1 (USNM); Santa Rosa Co., 2 (CNHM), 1* (CNHM); Volusia Co., 1 (MCZ); Wakulla Co., 5 (USNM), 3 (FSM); Cow Creek, 1* (CNHM). GEORGIA: Clarke Co., 2 (MMP), 1 (USNM); Charlton Co., 1

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[1] Wintering and migrant specimens were identified as individuals on the basis of physical characteristics.

(USNM); Echols Co., 1 (USNM); Richmond Co., 1 (USNM); Blackbeard Island, 1 (USNM). KENTUCKY: Hopkins Co., 1 (USNM). LOUISIANA: Baton Rouge Parish, 1 (CNHM), 2 (LSU); Orleans Parish, 1 (LSU), 1 (USNM); Ouachita Parish, 1 (LSU); St. John the Baptist Parish, 1 (LSU); Washington Parish, 1 (LSU); Chef Menteur, 1 (CNHM). MISSISSIPPI: Harrison Co., 4 (USNM), 1 (LSU); Jackson Co., 1 (CNHM); Warren Co., 1 (LSU); Lobdell, 1 (LSU). NORTH CAROLINA: Buncombe Co., 1 (USNM); Pasquotank Co., 1 (USNM); Rockingham Co., 1* (USNM); Wayne Co., 1 (USNM). SOUTH CAROLINA: Charleston Co., 1 (CHAM); Georgetown Co., 1 (USNM); Kershaw Co., 1 (USNM), 1* (USNM). TENNESSEE: Giles Co., 1 (USNM); Roane Co., 1 (USNM). TEXAS: Bee Co., 1 (AMNH); Cook Co., 1 (USNM); Galveston Co., 1 (AMNH). Hardin Co., 1 (AMNH). WEST VIRGINIA: Brooke Co., 1 (GMS).

Migrant Males. ALABAMA: Jackson Co., 1 (USNM); Tuscaloosa Co., 1 (USNM). CONNECTICUT: Windham Co., 2 (AMNH). FLORIDA: Alachua Co., 1 (DBUF); Dixie Co., 1 (FSM); Escambia Co., 1* (LSU); Nassau Co., 1 (AMNH); Wakulla Co., 1 (FSM). GEORGIA: Bullock Co., 1 (DZUG); Camden Co., 3 (MCZ); Chatham Co., 1* (USNM), 1 (USNM); Clarke Co., 7 (USNM); Cobb Co., 5 (CNHM), 1 (MMP); De Kalb Co., 1 (USNM); Fannin Co., 1 (USNM); Hall Co., 1 (USNM); Liberty Co., 1 (USNM); Thomas Co., 1 (AMNH); Union Co., 1 (USNM). ILLINOIS: Wabash Co., 1 (AMNH). KENTUCKY: Bell Co., 3 (USNM); Carroll Co., 1 (USNM); Hopkins Co., 1 (USNM); Rockcastle Co., 1 (USNM); Rowan Co., 1 (USNM); Trigg Co., 1 (USNM). LOUISIANA: East Baton Rouge Parish, 2 (LSU), 1* (LSU). MARYLAND: Cecil Co., 1 (AMNH); Montgomery Co., 2 (AMNH), 2 (CM); Prince George Co., 1 (AMNH). NEBRASKA: Lancaster Co., 1 (AMNH); Bald Island, 1 (USNM). NEW YORK: New York Co., 1 (AMNH); Queens Co., 1 (GMS); Suffolk Co., 2 (AMNH). NORTH CAROLINA: Buncombe Co., 1 (AMNH); Dare Co., 1 (USNM); Iredell Co., 1 (USNM); Pasquotank Co., 1 (USNM); Wake Co., 3 (NCS). PENNSYLVANIA: Erie Co., 1 (CM). SOUTH CAROLINA: Charleston Co., 4 (MCZ), 1 (CNHM); Cherokee Co., 1* (USNM); Georgetown Co., 1 (USNM); Richland Co., 1 (CNHM). TENNESSEE: Fayette Co., 2 (USNM); Lake Co., 1 (USNM); Lincoln Co., 1 (USNM); Obion Co., 1 (USNM); Roane Co., 2 (USNM); Stewart Co., 1 (USNM). VIRGINIA: Alexandria Co., 3 (USNM); Arlington Co., 1 (USNM); Essex Co., 1 (USNM); Fairfax Co., 2* (MCZ), 5 (USNM); Orange Co., 1 (USNM). WEST VIRGINIA: Cabell Co., 1 (USNM); Greenbriar Co., 1 (AMNH); Logan Co., 1 (USNM).

Migrant Females. ALABAMA: Colbert Co., 2 (USNM); Walker Co., 1 (USNM); Sand Mt. 1 (USNM). FLORIDA: Alachua Co., 2 (FSM), 1 (JCD); Wakulla Co., 1 (FSM). GEORGIA: Chatham Co., 1 (MCZ); Clarke Co., 1 (USNM); Cobb Co., 1 (CNHM). ILLINOIS: Wabash Co., 1 (USNM). KENTUCKY: Carroll Co., 1 (USNM); Mead Co., 1 (USNM); Trigg Co., 1 (USNM). LOUISIANA: Orleans Parish, 1 (LSU). MICHIGAN: Jackson Co., 1 (GMS). MISSISSIPPI: Bolivar Co., 1 (USNM), 1* (USNM); Harrison Co., 2 (LSU), 4 (USNM). NEW JERSEY: Morris Co., 1 (AMNH). NEW YORK: Orange Co., 1 (USNM); Queens Co., 1 (AMNH); Dunwoodie, 1 (AMNH). NORTH CAROLINA: Charleston Co., 2 (USNM). TENNESSEE: Carter Co., 1* (USNM); Roane Co., 1 (USNM); Shelby Co., 1 (USNM); Union Co., 1 (UMMZ). TEXAS: Chambers Co., 1 (AMNH). VIRGINIA: Fairfax Co., 2 (USNM); Surrey Co., 1 (USNM). WASHINGTON, D. C.: 1 (USNM). WEST VIRGINIA: Cabell Co., 1 (USNM); Logan Co., 1 (USNM); Pendleton Co., 1 (USNM); Rorer, 1 (CM); Fourleen, 1 (USNM).

PIPILO ERYTHROPHTHALMUS ALLENI Coues

Pipilo alleni Coues (1871: 366, footnote), original description. Type locality: Dummitt's Grove, Indian River, Florida.

Pipilo erythrophthalmus var. *alleni*, Baird, Brewer, and Ridgway (1874: 112).

Pipilo leucopis Maynard (1878: 113, pl. IV), original description. Type locality: Dummitt's Grove, Florida.

Pipilo erythrophthalmus subsp. *Pipilo alleni*, Sharpe (1888: 746).

Description

Diagnosis. A small, medium-billed, pale-eyed race, showing very little white on the rectrices.

Average dimensions of males. Wing, 80.47 ± .29 (σ, 2.62); tail, 91.43 ± .42 (σ, 3.74); exposed culmen, 15.05 ± .07 (σ, 0.61); width of lower mandible, 8.48 ± .04 (σ, 0.33); tarsus, 26.78 ± .11 (σ, 0.95); middle toe without claw, 18.88 ± .09 (σ, 0.81); length of white on inner web of outermost rectrix, 19.71 ± .50 (σ, 4.44). (See Table 3).

Average dimensions of females. Wing, 76.50 ± .41 (σ, 2.08); tail, 85.42 ± .67 (σ, 3.40); exposed culmen, 14.71 ± .10 (σ, 0.48); width of lower mandible, 8.47 ± .06 (σ, 0.28); tarsus, 25.89 ± .17 (σ, 0.89); middle toe without claw, 18.57 ± .14 (σ, 0.71); length of white on inner web of outermost rectrix, 15.58 ± .69 (σ, 3.52). (See Table 4.)

Average color of males. Back, Iron Gray; flanks ,12-F-10; breast, Iron Gray; top of head, Iron Gray.

Average color of females. Back, 15-E-7; flanks, 13-D-11; breast, 14-J-9; top of head, 15-E-12.

Table 3
P. e. alleni
Males

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	82	80.47	.29	2.62	77.85–83.08	73.0– 89.0
Tail	81	91.43	.42	3.79	87.69–95.17	78.0–102.2
Tail Spot	78	19.71	.50	4.44	15.26–24.15	6.1– 27.5
Culmen	80	15.05	.07	.61	14.44–15.65	13.9– 16.1
Mandible Width	82	8.48	.04	.33	8.15– 8.81	7.6– 9.5
Tarsus	81	26.78	.11	.95	25.84–27.73	24.7– 29.1
Middle Toe	81	18.88	.10	.81	18.07–19.70	17.0– 21.0

Table 4
P. e. alleni
Females

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	26	76.50	.41	2.08	74.42–78.58	73.0–81.5
Tail	26	85.43	.67	3.40	82.03–88.82	79.3–92.1
Tail Spot	26	15.58	.69	3.52	12.06–19.09	6.0–20.2
Culmen	25	14.71	.10	.48	14.23–15.19	13.1–15.5
Mandible Width	22	8.47	.06	.28	8.19– 8.74	8.0– 9.0
Tarsus	26	25.89	.17	.89	25.00–26.77	24.2–28.0
Middle Toe	26	18.57	.14	.71	17.85–19.28	17.0–20.0

Iris color. Straw.

Breeding range. Florida (from Bay, Franklin, Levy, Alachua and Putnam Counties south through the peninsula); absent from the Florida Keys. (See Map 2.)

Winter range. In Florida (from Santa Rosa, Franklin, Leon, Columbia and Duval Counties south through the peninsula); absent from the Florida Keys. (See Map 3.)

Comments. P. e. alleni is the best defined of the four races of *P. erythrophthalmus.* The uniformity of iris color, small amount of white on the outermost rectrix and the short wing make this race easily recognized.

Its habitat preference during the breeding season varies with locality. Along the coast the towhee is the commonest bird of the dune association of *Quercus geminata, Q. myrtifolia, Pinus clausa, Serenoa repens* and *Ceratiola ericoides.* This same scrub habitat, inland, is also heavily populated with *P. e. alleni.* In areas where scrub does not occur the birds are found in second-growth associations which approximate the natural scrub habitat in physical aspect. Often large numbers are found in close proximity to cities and towns, where cultivation has created similar conditions.

During the winter *alleni* does not seem to be so specific in its habitat demands, and is found in a great variety of situations. Individuals have been taken in urban areas, pine flatwoods, mesophytic hammocks, tropical hammocks and mangrove bays. During this season flocks of fifteen or twenty birds are not uncommon and on some occasions these flocks may contain resident and migrant individuals.

Specimens Examined

Atypical specimens are indicated as follows:

**alleni* > *rileyi*

Breeding Males. FLORIDA: Alachua Co., 1 (AMNH), 1 (BDUF), 2 (PB), 2 (JCD); Bay Co., 1* (UMMZ); Brevard Co., 3 (AMNH), 3 (CNHM), 1* (CNHM), 1 (USNM), 2 (MCZ), 1 (PB), 1 (JCD); Broward Co., 2 (PB), 1 (JCD); Charlotte Co., 2 (CM); Collier Co., 1 (USNM); Dade Co., 1 (JCD), 1 (USNM), 1 (UMMZ); Franklin Co., 1 (LSU), 2 (JCD), 1* (JCD); Highlands Co., 1 (USNM); Hillsborough Co., 4 (JCD); Lee Co., 3 (JCD); Levy Co., 3 (JCD); Martin Co., 1 (JCD); Palm Beach Co., 1 (CM), 1 (USNM); Pasco Co., 2 (USNM); Pinellas Co., 4 (MCZ); 1 (UMMZ), 2 (AMNH), 4 (USNM); Polk Co., 5 (JCD); Putnam Co., 4 (GN), 1 (USNM), 1* (JCD); Saint Lucie Co., 1 (AMNH); Sarasota Co., 1 (AMNH); Volusia Co., 6 (AMNH).

Breeding Females. FLORIDA: Alachua Co., 1 (JCD); Benton, 1 (USNM); Brevard Co., 1 (AMNH); Broward Co., 4 (JCD); Charlotte Co., 1 (CM); 1 (JCD); Hillsborough Co., 2 (JCD); Highlands Co., 1 (LSU); Levy Co., 2 (JCD); Nassau Co., 1 (USNM); Orange Co., 1 (CM); Pinellas Co., 1 (AMNH), 1 (MCZ); 4 (USNM); Polk Co., 1 (JCD); Putnam Co., 1 (GN); Volusia Co., 1 (AMNH), 1 (MCZ).

Wintering Males. FLORIDA: Alachua Co., 3 (AMNH), 1* (AMNH), 4 (JCD), 1(PB); Brevard Co., 1 (MMP), 1 (MCZ), 3 (CNHM), 1* (CM), 2 (USNM), 18 (AMNH); Charlotte Co., 1 (UMMZ), 9 (MCZ); Collier Co., 1 (MMP), 4 (USNM); Columbia Co., 2 (LSU); Escambia Co., 1* (LSU); Franklin Co., 1 (LSU); Hernando Co., 1 (JCD), 1 (PB); Highlands Co., 6 (USNM); Hillsborough Co., 1 (CM); Indian River Co., 1 (LSU); Lake Co., 1 (JCD); Lee Co., 2 (AMNH), 4 (CNHM); Leon Co., 1 (USNM); Levy Co., 2 (MCZ), 1* (MCZ), 1 (PB), 2 (JCD), 6 (AMNH), 1* (AMNH); Nassau Co., 3 (CNHM), 1* (CNHM); Okaloosa Co., 1 (USNM); Okeechobee Co., 3 (USNM); Orange Co., 3 (GMS); Osceola Co., 3 (USNM), 1* (USNM); Palm Beach Co., 5 (CNHM); Pinellas Co., 4 (AMNH), 4 (MCZ), 1* (MCZ), 2 (CNHM), 1 (FSM), 7 (UMMZ); Polk Co., 1 (USNM), 2 (UMMZ); Putnam Co., 3 (CNHM), 1* (CNHM); Santa Rosa Co., 2 (CNHM), 2* (CNHM); St. Lucie Co., 1 (USNM); Volusia Co., 2 (AMNH), 1 (MCZ). GEORGIA: Camden Co., 1* (AMNH), 1* (MCZ), 1 (USNM); Chatham Co., 1* (LSU); Liberty Co., 1* (DZUG), 1* (USNM).

Wintering Females. FLORIDA: Brevard Co., 1 (AMNH), 3 (CNHM), 1* (CNHM); Collier Co., 2 (USNM); Dade Co., 1 (UMMZ); Desoto Co., 2 (USNM); Duval Co., 1* (MCZ); Franklin Co., 1 (MMP), 1 (LSU); Highlands Co., 1 (USNM); Indian River Co., 3 (MCZ); Lee Co., 1 (CNHM), 6 (MCZ); Nassau Co., 1 (CNHM); Orange Co., 1 (GMS); Osceola Co., 1 (USNM); Okaloosa Co., 1 (USNM); Palm Beach Co., 1 (USNM), 2 (CNHM); Pinellas Co., 1 (AMNH), 1 (CNHM), 4 (UMMZ), 1* (UMMZ), 3 (MCZ); Putnam Co., 3 (CNHM); Santa Rosa Co., 2 (CNHM), 4* (CNHM); Volusia Co., 2 (MCZ), 1 (AMNH); Kissimmee Prairie, 1 (USNM), 1 (MCZ). GEORGIA: Camden Co., 1* (MCZ); Chatham Co., 1* (CHAM); Levy Co., 1* (MCZ).

Migrant Females. FLORIDA: Brevard Co., 1 (CNHM); Lee Co., 1 (MCZ); Orange Co., 1 (MMP); Palm Beach Co., 2 (CNHM); Pinellas Co., 1 (MCZ), 1 (UMMZ).

PIPILO ERYTHROPHTHALMUS CANASTER Howell

Pipilo erythrophthalmus var. *erythrophthalmus*, Baird, Brewer, and Ridgway (1874: 108), part.

Pipilo erythrophthalmus canaster Howell (1913: 202), original description. Type locality: Spring Hill, Alabama.

Pipilo erythrophthalmus leptoleucus Oberholser (1938: 641), original description. Type locality: New Orleans, Louisiana.

Description

Diagnosis. A large, large-billed, pale race, with variable eye color, showing a medium amount of white on the rectrices.

Average dimensions of males. Wing, 87.30 ± .21 (σ, 2.50); tail, 94.95 ± .30 (σ, 3.53); culmen, 15.44 ± .05 (σ, 0.60); width of lower mandible, 8.94 ± .03 (σ, 0.37); tarsus, 20.19 ± .08 (σ, 1.00); middle toe without claw, 20.19 ± .07 (σ, 0.88); length of white on inner web of outermost rectrix, 31.79 ± .40 (σ, 4.71); tail spot/tail ratio, 35.59 ± .45 (σ, 5.17). (See Table 5.)

Average dimensions of females. Wing, 83.45 ± .42 (σ, 2.31); tail, 90.43 ± .02 (σ, 3.37); culmen, 15.20 ± .10 (σ, 0.55); width of lower mandible, 8.79 ± .07 (σ, 0.36); tarsus, 27.91 ± .20 (σ, 1.03); middle toe without claw, 19.66 ± .16 (σ, 0.85); length of white on inner web of outermost rectrix, 26.98 ± .70 (σ, 3.64); tail spot/tail ratio, 29.41 ± .74 (σ, 3.87). (See Table 6.)

Average color of males. Back, Olivaceous Black (3); flanks, 13-D-11; breast, Olivaceous Black (3); top of head, Olivaceous Black (3).

Table 5
P. e. canaster
Males

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	145	87.30	.21	2.50	84.81–89.80	78.0– 93.0
Tail	136	94.95	.30	3.53	91.42–98.48	86.0–105.0
Tail Spot	136	31.79	.40	4.71	27.08–36.51	18.0– 43.6
Culmen	142	15.44	.05	.50	14.85–16.04	14.5– 17.0
Mandible Width	141	8.94	.03	.37	8.57– 9.30	8.2– 9.7
Tarsus	145	28.19	.08	1.00	27.19–29.19	25.2– 31.0
Middle Toe	145	20.19	.07	.88	19.31–21.07	18.0– 22.5
Tail Spot/Tail	130	35.59	.45	5.17	27.42–37.76	19.0– 45.0

Average color of females. Back, 15-E-7; flanks, 13-K-9; breast, 15-C-12; top of head, 7-A-12.

Iris color. Variable, red to pale orange, occasionally yellow. (See Table 21.)

Breeding range. From eastern Louisiana (Iberia, Pointe Coupee, and West Carroll Parishes), and western Mississippi (Bolivar County),

Table 6
P. e. canaster
Females

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	31	83.45	.42	2.31	81.14–85.76	79.5–87.0
Tail	27	90.43	.62	3.37	87.06–93.80	83.5–96.0
Tail Spot	25	26.98	.70	3.64	23.35–30.62	18.8–35.6
Culmen	27	15.20	.10	.55	14.67–15.75	14.0–16.5
Mandible Width	28	8.79	.07	.36	8.43– 9.16	8.2– 9.4
Tarsus	27	27.91	.20	1.03	26.88–28.94	25.6–29.5
Middle Toe	27	19.66	.16	.85	18.82–20.51	17.6–21.0
Tail Spot/Tail	27	29.41	.74	3.87	25.54–33.27	22.0–39.0

north to southern Tennessee (Shelby and Wayne Counties), northern Alabama (Colbert, Limestone, Shelby, and Calhoun Counties), and central Georgia (Chattooga, Floyd, Paulding, Cobb, Gwinnett, Jackson, Clarke, and Oglethorpe Counties to Taliaferro, Hancock, Putman, Jasper, Lamar, and Merriwether Counties), south to middle eastern Alabama (Russell and Montgomery Counties), thence south to the Gulf Coast, in western Florida (Okaloosa and Santa Rosa Counties), southern Alabama, Mississippi, and southeastern Louisiana (St. Bernard, Assumption, and Iberia Parishes). Also in central-southern North Carolina (Richmond County). (See Map 2.)

Winter range. From southeastern Louisiana, central Mississippi (Warren County), central Alabama (Jefferson County), and northern Georgia (Rabun County), to coastal South Carolina (Beaufort, Charleston, and Georgetown Counties) and eastern North Carolina (Pitt County), south to southern Georgia (Toombs, Lowndes, and Brooks Counties), to western Florida (Wakulla and Leon Counties), and thence westward along the Gulf to southeastern Louisiana. (See Map 3.)

Comments. The habitat preference of this form as noted near the type locality is apparently slightly different from that of *P. e. alleni* or *P. e. rileyi*. Exploration of what appeared to me to be suitable habitats, on the basis of my own experience in Florida, produced not a single towhee. Specimens taken near Mobile, Alabama, came from extremely dense hammock-like habitats.

This form is not completely sedentary in its habits, but on the other hand it does not move as far south in winter as do *erythrophthalmus* and *rileyi*.

Specimens Examined

Atypical specimens are indicated as follows:

* *canaster* > *rileyi*
** *canaster* > *erythrophthalmus*

Breeding males. ALABAMA: Baldwin Co., 1 (UMMZ); Calhoun Co., 2 (USNM); Colbert Co., 3 (USNM); Limestone Co., 3 (USNM); Mobile Co., 4 (USNM), 2 (JCD), 1 (LSU); Russell Co., 1 (USNM); Shelby Co., 2 (USNM). FLORIDA: Okaloosa Co., 3* (CM), 1 (JCD); Santa Rosa Co., 1 (JCD), 1 (USNM). GEORGIA: Carroll Co., 1 (USNM); Chatooga Co., 2 (USNM); Clarke Co., 2 (LSU), 1 (MMP), 9 (USNM), 1** (USNM), 2* (USNM); Clayton Co., 2 (USNM); Cobb Co., 1 (USNM), 1* (USNM); DeKalb Co., 2 (LSU), 1* (MMP), 4 (USNM); Douglas Co., 1 (USNM); Floyd Co., 2 (USNM); Fulton Co., 2 (MMP), 2 (USNM), 1** (USNM); Gwinnett Co., 2 (USNM); Hancock Co., 1 (USNM); Haralson Co., 1 (USNM); Henry Co., 1 (USNM), 1* (USNM); Jackson Co., 3 (USNM); Jasper Co., 1 (USNM); Lamar Co., 1* (USNM); Meriweather Co., 1 (USNM); Morgan Co., 1 (USNM); Oglethorpe Co., 1 (USNM); Paulding Co., 2 (USNM); Putnam Co., 1 (USNM); Rockdale Co., 1 (USNM); Taliaferro Co., 2 (USNM); Walton Co., 1 (USNM.) LOUISIANA: Assumption Parish, 1 (LSU), East Baton Rouge Parish, 2 (LSU), 5 (USNM); Iberia Parish, 1 (MMP); Orleans Parish, 7 (USNM), 6 (LSU), 1 (MMP); Pointe Coupee Parish, 1 (GMS); Saint Bernard Parish, 2 (USNM); West Baton Rouge Parish, 1 (CHAM); West Carroll Parish, 1 (LSU); West Feliciana Parish, 1 (USNM). MISSISSIPPI: Adams Co., 2 (USNM); Bolivar Co., 1 (USNM), 1 (CNHM); Hancock Co., 1 (USNM); Harrison Co., 4 (LSU), 11 (USNM); Warren Co., 1 (USNM). TENNESSEE: Shelby Co., 3 (LSU); Wayne Co., 3 (USNM).

Breeding Females. ALABAMA: Calhoun Co., 1 (USNM); Mobile Co., 1 (USNM), 1 (JCD); Russell Co., 1 (USNM). FLORIDA: Okaloosa Co., 1 (CM). GEORGIA: Clarke Co., 2 (MMP), 1 (USNM); Cobb Co., 1 (CNHM), 2 (USNM); DeKalb Co., 2 (USNM); Fayette Co., 1 (USNM); Fulton Co., 1 (MMP), 2 (USNM); Hancock Co., 1 (USNM); Oglethorpe Co., 1 (USNM); Taliaferro Co., 1 (USNM). LOUISIANA: East Baton Rouge Parish, 1 (USNM); Orleans Parish, 1 (USNM); Pointe Coupee Parish, 1 (GMS). MISSISSIPPI: Bolivar Co., 1 (CNHM); Harrison Co., 3 (USNM); Pearl River Co., 1 (AMNH). NORTH CAROLINA: Richmond Co., 1 (USNM).

Wintering Males. ALABAMA: Baldwin Co., 1 (USNM); Jefferson Co., 1 (LSU); Lee Co., 1 (USNM); Mobile Co., 1 (LSU). FLORIDA:

Leon Co., 1 (CNHM); Okaloosa Co., 3 (CM); Santa Rosa Co., 2 (CNHM);Wakulla Co., 1 (USNM). GEORGIA: Barrow Co., 1 (USNM); Brooks Co., 1 (USNM); Clarke Co., 6 (USNM); DeKalb Co., 2 (USNM), 1 (DZUG); Fulton Co., 2 (USNM); Lowndes Co., 1 (USNM); Madison Co., 2 (USNM); Oconee Co., 2 (USNM); Walton Co., 1 (USNM). LOUISIANA: East Baton Rouge Parish, 3 (LSU), 1 (USNM); Orleans Parish, 3 (LSU), 2 (CNHM). MISSISSIPPI: Amite Co., 1 (USNM); Forrest Co., 1 (LSU); Harrison Co., 1 (LSU), 6 (USNM); Rankin Co., 1 (MMP); Warren Co., 1 (LSU). NORTH CAROLINA: Pitt Co., 1 (USNM). SOUTH CAROLINA: Beaufort Co., 1 (CHAM), 1 (MCZ).

Wintering Females. ALABAMA: Houston Co., 4 (USNM); Orange Beach, 1 (USNM). FLORIDA: Escambia Co., 1 (USNM); Leon Co., 1* (CNHM); Okaloosa Co., 1 (CM); Santa Rosa Co., 1 (CNHM); 1* (CNHM); Wakulla Co., 1 (FSM), 1* (USNM). GEORGIA: Cobb Co., 1 (CNHM), 1* (CNHM); DeKalb Co., 1 (USNM); Rabun Co., 1 (USNM). LOUISIANA: East Baton Rouge Parish, 1 (CNHM), 1 (LSU), 1 (USNM); Orleans Parish, 1 (LSU), 2 (USNM); Chef Menteur, 1 (CNHM). MISSISSIPPI: Harrison Co., 4 (LSU), 1 (USNM); Rankin Co., 1 (MMP). SOUTH CAROLINA: Charleston Co., 1 (CHAM); Georgetown Co., 1* (USNM).

Migrant Males. ALABAMA: Baldwin Co., 2* (USNM); Mobile Co., 1* (USNM); FLORIDA: Escambia Co., 1 (USNM); Okaloosa Co., 1 (CM). GEORGIA: Clarke Co., 2 (USNM); Cobb Co., 2 (CNHM); DeKalb Co., 1 (USNM); Harris Co., 1 (USNM); Jefferson Co., 1 (USNM); Toombes Co., 1 (USNM); Treutlen Co., 1 (USNM); Washington Co., 1 (USNM). LOUISIANA: East Baton Rouge Parish, 1 (LSU), 2 (USNM); Orleans Parish, 2 (LSU); West Feliciana Parish, 1 (GMS). MISSISSIPPI: Harrison Co., 1 (USNM), 2* (USNM), 1 (MMP); Pearl River Co., 1 (AMNH); Warren Co., 2 (CNHM). NORTH CAROLINA: Carteret Co., 1* (USNM). SOUTH CAROLINA: Georgetown Co., 1 (USNM). TENNESSEE: Roane Co., 1 (USNM).

Migrant Females. GEORGIA: Clarke Co., 1 (MMP); Harris Co., 1 (USNM). LOUISIANA: East Baton Rouge Parish, 1 (USNM); Orleans Parish, 1 (LSU). MISSISSIPPI: Harrison Co., 2 (USNM).

PIPILO ERYTHROPHTHALMUS RILEYI Koelz

Pipilo leucopis Maynard (1878: 113, pl. IV), part.

Pipilo erythrophthalmus var. *alleni*, Baird, Brewer, and Ridgway (1874: 112), part.

Pipilo alleni Koelz (1939: 121), original description. Type locality: Brunswick, Georgia.

Description

Diagnosis. A medium-sized, large-billed race, with variable eye color, and showing less white on the rectrices than its northern relatives.

Average dimensions of males. Wing, 85.53 ± .26 (σ, 2.62); tail, 94.59 ± .36 (σ, 3.43); culmen, 15.64 ± .62 (σ, 0.62); width of lower mandible, 8.85 ± .03 (σ, 0.31); tarsus, 28.25 ± .10 (σ, 0.99); middle toe without claw, 19.89 ± .07 (σ, 0.68); length of white on inner web of outermost rectrix, 25.50 ± .41 (σ, 3.72). (See Table 7.)

Average dimensions of females. Wing, 80.32 ± .46 (σ, 2.81); tail 89.70 ± .67 (σ, 3.67); exposed culmen, 15.34 ± .09 (σ, 0.53); width of lower mandible, 8.69 ± .05 (σ, 0.27); tarsus, 27.54 ± .19 (σ, 1.15); middle toe without claw, 19.38 ± .11 (σ, 0.67); length of white on inner web of outermost rectrix, 22.85 ± .61 (σ, 2.93). (See Table 8.)

Average color of males. Back, Olivaceous Black; flanks, 13-D-11; breast, Olivaceous Black; top of head, Olivaceous Black.

Average color of females. Back, 15-C-11; flanks, 13-K-11; breast, 15-C-9; top of head, 8-H-11.

Table 7
P. e. rileyi
Males

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	100	85.54	.26	2.62	82.91–88.15	80.0– 92.0
Tail	91	94.59	.36	3.43	91.16–93.03	87.0–103.0
Tail Spot	84	25.50	.41	3.71	21.78–29.22	17.0– 34.0
Culmen	98	15.64	.06	.62	15.01–16.26	14.1– 17.0
Mandible Width	96	8.85	.03	.31	8.54– 9.16	8.0– 9.5
Tarsus	100	28.25	.10	.99	27.26–29.24	25.3– 30.6
Middle Toe	100	19.89	.07	.68	19.21–20.57	17.0– 21.5

Iris color. Variable, straw to orange or red. (See Table 21).

Breeding range. From western Florida (Walton County), southeastern Alabama (Houston County), northeast through southeastern Georgia (Early, Dougherty, Crisp, Jones, Warren, McDuffie and Richmond Counties) to coastal South Carolina (Jasper, Beaufort, Charleston, and Georgetown Counties) and coastal North Carolina (Brunswick, New Hanover and Carteret Counties) south along the coast of

Table 8
P. e. rileyi
Females

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	38	80.32	.46	2.81	77.51–83.13	72.5–85.0
Tail	30	89.70	.67	3.66	86.04–93.36	80.9–97.0
Tail Spot	23	22.84	.61	2.93	19.92–25.78	19.9–30.3
Culmen	38	15.34	.09	.53	14.81–15.87	14.5–16.5
Mandible Width	37	8.69	.05	.27	8.42– 8.96	8.2– 9.4
Tarsus	36	27.54	.19	1.15	26.39–28.69	25.4–29.6
Middle Toe	38	19.38	.11	.67	18.71–20.06	17.5–20.5

Georgia (Chatham, Glynn and Camden Counties) thence west through southern Georgia (Charlton County) and northern Florida (Madison and Leon Counties) to the Gulf Coast (Wakulla County). (See Map 2.)

Winter range. From western Florida (Escambia County), eastern Alabama (Lee County) north to north-central Georgia (Cobb, Walton and Clarke Counties) to coastal South Carolina (Beaufort, Jasper, Dorchester, Charleston and Georgetown Counties) and eastern North Carolina (Robeson, Carteret, Pitt and Hyde Counties) south to mid-peninsular Florida (Brevard, Charlotte and Pinellas Counties). (See Map 3.)

Comments. This pale-eyed race is clearly distinguished from *P. e. alleni* by its larger wing and greater amount of white on the rectrices. It can be distinguished from *P. e. erythrophthalmus* and *P. e. canaster* by the color of its irides and by the intermediate amount of white present on the rectrices. The color of the flanks in *rileyi*, especially in the males, is remarkably uniform in the material examined and is much darker than that found in *P. e. alleni.*

My experience with this race at the type locality during the breeding season agrees with that of Walter Koelz, the original describer. The preferred habitat is in scrubby, moderately dense growth. Specimens were taken on St. Simons Island, and on the mainland a few miles to the north and south of Brunswick, Georgia, in much the same type of habitat that is preferred by *P. e. alleni* in Florida. Material from west Florida, in Walton County, was also taken in this same scrub association.

Specimens Examined

Atypical specimens are indicated as follows:

* *rileyi* > *canaster*
** *rileyi* > *erythrophthalmus*
*** *rileyi* > *alleni*

Breeding Males. ALABAMA: Houston Co., 1 (USNM). FLORIDA: Leon Co., 4 (USNM); Madison Co., 1 (USNM); Walton Co., 6 (JCD), 1* (JCD), 1 (AMNH). SOUTH CAROLINA: Beaufort Co., 1 (MCZ), 1 (AMNH), 1 (USNM); Charleston Co., 1 (CHAM), 1** (CHAM), 3 (MCZ), 1* (MCZ), 2 (USNM); Georgetown Co., 1 (USNM), 1* (USNM); Jasper Co., 1 (USNM). NORTH CAROLINA: Brunswick Co., 2** (NCS); Carteret Co., 1 (NCS); New Hanover Co., 1 (USNM), 1* (USNM). GEORGIA: Baker Co., 3 (DZUG), 2 (USNM); Ben Hill Co., 1 (USNM); Bibb Co., 1 (USNM); Bullock Co., 1 (USNM); Burke Co., 1 (USNM), 1* (USNM); Camden Co., 1 (DZUG), 1 (MCZ); Candler Co., 1 (USNM); Charlton Co., 1 (DZUG), 1 (USNM); Chatham Co., 1 (CHAM), 3 (USNM); Coffee Co., 1 (USNM); Colquitt Co., 1 (USNM); Cook Co., 1 (USNM); Crisp Co., 2 (USNM); Decatur Co., 1 (DZUG); Dodge Co., 1 (USNM); Dougherty Co., 1* (USNM), 1 (DZUG); Early Co., 1 (DZUG); Effingham Co., 1 (USNM); Glynn Co., 7 (JCD), 1 (PB), 1 (DZUG); Grady Co., 1*** (USNM); Irwin Co., 1 (USNM); Jones Co., 1 (LSU), 2 (USNM); Lowndes Co., 1 (USNM); Macduffie Co., 1 (MMP); Pierce Co., 1 (USNM); Pulaski Co., 1 (USNM); Richmond Co., 1 (MMP), 3 (USNM); Thomas Co., 2 (USNM), 1* (USNM); Turner Co., 1 (USNM); Ware Co., 2 (USNM); Warren Co., 1* (USNM).

Breeding Females. FLORIDA: Franklin Co., 1 (USNM); Leon Co., 1* (USNM); Walton Co., 5 (JCD), 1* (USNM). GEORGIA: Bacon Co., 1 (USNM); Baker Co., 1 (DZUG), 1 (USNM); Ben Hill Co., 1 (USNM); Brantly Co., 1 (DZUG); Candler Co., 1 (USNM); Chatham Co., 1 (USNM); Colquitt Co., 1 (USNM); Cook Co., 1 (USNM); Crisp Co., 1 (USNM); Decatur Co., 1 (DZUG); Dodge Co., 1 (USNM) Dougherty Co., 2 (DZUG); Glynn Co., 3 (JCD), 1 (PB); Grady Co., 1 (USNM); McDuffie Co., 1 (USNM); Sumter Co., 1 (MMP); Ware Co., 1 (USNM). NORTH CAROLINA; Brunswick Co., 1 (USNM); Carteret Co., 1 (USNM). SOUTH CAROLINA: Charleston Co., 1 (MCZ), 1** (MCZ), 2 (USNM); Georgetown Co., 1 (USNM).

Wintering Males. ALABAMA: Lee Co., 2 (UMMZ). FLORIDA: Alachua Co., 1 (AMNH); Baker Co., 1 (USNM); Brevard Co., 2 (CNHM); Charlotte Co., 1 (MCZ); Columbia Co., 1 (LSU); Duval Co., 1 (USNM); Escambia Co., 1 (LSU), 1 (USNM); Franklin Co., 2 (LSU), 1 (USNM); Hamilton Co., 1 (USNM); Levy Co., 4 (AMNH); Nassau Co., 2 (AMNH); Okaloosa Co., 9 (CM); Pinellas Co., 1 (AMNH); Putnam Co., 1 (CNHM); Santa Rosa Co., 12 (CNHM); Walton Co., 1 (USNM). GEORGIA: Berrien Co., 1 (USNM); Calhoun Co., 1 (USNM); Camden Co., 1 (DZUG), 2 (MCZ), 5 (AMNH); Charlton Co., 3 (USNM); Chatham Co., 2 (USNM), 4 (CHAM); Clarke Co., 1 (USNM); Echols Co., 1 (DZUG), 1 (USNM); Glynn Co., 1 (LSU), 1 (MMP), 1 (UMMZ); Liberty Co., 1 (USNM); McIntosh Co., 2 (AMNH); Tatnall Co., 1 (USNM); Walton Co., 1 (USNM). NORTH CAROLINA: Carteret Co., 3 (USNM); Pitt Co., 2 (USNM). SOUTH CAROLINA: Beaufort Co., 5 (MCZ), 2 (USNM), 1 (AMNH); Charleston Co., 6 (CHAM), 2 (USNM); Georgetown Co., 1 (USNM).

Wintering Females. FLORIDA: Alachua Co., 1 (CNHM), 1 (USNM); Brevard Co., 1 (MCZ); Escambia Co., 1 (LSU), 1 (USNM); Levy Co., 1 (AMNH); Nassau Co., 1 (CNHM); Okaloosa Co., 7 (CM); Columbia Co., 1 (LSU); Pinellas Co., 1 (CNHM); Santa Rosa Co., 9 (CNHM); Volusia Co., 1 (MCZ); Wakulla Co., 1 (FSM), 1 (USNM); Walton Co., 1 (USNM). GEORGIA: Berrien Co., 1 (USNM); Brooks Co., 1 (USNM); Camden Co., 1 (MCZ); Chatham Co., 2 (CHAM); Clarke Co., 2 (USNM); Echols Co., 1 (DZUG); Glynn Co., 1 (LSU), 1 (MMP), 1 (UMMZ); Hinesville, 1 (USNM). NORTH CAROLINA: Carteret Co., 2 (USNM); Hyde Co., 1 (USNM); Robeson Co., 1 (CNHM). SOUTH CAROLINA: Charleston Co., 3 (CHAM); Dorchester Co., 1 (CHAM); Georgetown Co., 1 (USNM); Jasper Co., 2 (USNM).

Migrant Males. FLORIDA: Levy Co., 1 (AMNH); Okaloosa Co., 1 (CM); Santa Rosa Co., 1 (USNM), 2 (CNHM). GEORGIA: Bryan Co., 1 (USNM); Camden Co., 1 (USNM); Chatham Co., 1 (MCZ); Cobb Co., 1 (CNHM); Cook Co., 1 (MMP); Decatur Co., 1 (DZUG); Evans Co., 1 (USNM); Liberty Co., 2 (USNM); Long Co., 1 (USNM); McIntosh Co., 1 (UMMZ); Tatnall Co., 1 (DZUG), 1 (USNM); Telfair Co., 1 (USNM); Thomas Co., 1 (AMNH); Washington Co., 1 (USNM). NORTH CAROLINA: Pitt Co., 1* (USNM). SOUTH CAROLINA: Charleston Co., 1 (CNHM), 3 (MCZ); Georgetown Co., 1 (USNM).

Migrant Females. FLORIDA: Escambia Co., 2 (USNM); Franklin Co., 1 (JCD); Okaloosa Co., 1 (CM); Santa Rosa Co., 2 (CNHM), 1 (USNM). GEORGIA: Camden Co., 2 (MCZ), 1 (USNM); Cook Co., 1 (MMP); Fulton Co., 1 (USNM); Tatnall Co., 1 (USNM); Treutlen Co., 1 (USNM). SOUTH CAROLINA: Beaufort Co., 1 (MCZ), Charleston Co., 1 (MCZ), 2 (USNM); Georgetown Co., 1* (USNM); Greenville Co., 1* (USNM).

GEOGRAPHIC VARIATION

Following preliminary examination, the material at hand was separated into six samples (Map 1). Mean, standard error of the mean, and standard deviation of the mean were calculated for each of the mensural characters investigated. These samples were treated separately for each sex, except for samples 1, 2 and 3, of which only the males were considered (Tables 9, 10 and 11). For each sex samples 1, 2 and 3 were later treated as a single sample, representing the northern population, *P. e. erythrophthalmus.* For greater clarity, these three northern samples are referred to in the following discussion as eastern, central and western, respectively. Sample 4 represents *P. e. canaster,* 5 represents *P. e. rileyi,* and 6 represents *P. e. alleni.*

Means were regarded as being significantly different when two standard errors on either side of the means did not overlap in the samples under consideration. A character was assumed to be of diagnostic value if it furnished more than 75 per cent correct separation of mixed samples.

The degrees of separation furnished by the various characters are presented in Tables 12–19. In these tables, the distance in standard units to the point of intersection of the standard distributions is represented by d/σ. *Per cent separation* is the measure of area of the standard curves which lie to either side of the point of intersection of these curves. *Division point* is the theoretical point of maximum separation in millimeters for each of the characters indicated. X indicates that the difference is not statistically significant, and Z indicates that the degree of separation accomplished by the character is less than 50.0 per cent.

Figures 1–15 present this same information in the form of Hubbs-Perlmutter diagrams. For a discussion of the use of this method of demonstrating differences between populations see Hubbs and Perlmutter (1942). In each diagram a vertical line marks the mean; a rectangle to either side indicates one standard deviation; the black part of each rectangle indicates twice the standard error of the mean; a solid line shows the observed range of variation; a broken line shows the limits of three standard deviations to either side of the mean, beyond observed range.

Wing Length

Males (Figure 1). Among the four races here recognized, *erythrophthalmus* has the longest wing, 87.57 ± .15 mm. This form represents the northern part of the range of the species and extends from the eastern seaboard to the junction with *Pipilo arcticus maculatus* on the west. It shows a gradual increase in wing length from east to west. The eastern sample shows a mean wing length of 86.63 ± .16 mm., the central sample 87.32 ± .28 mm., and the western sample 89.77 ± .28 mm. The difference in the means of the eastern and central samples is not statistically significant.

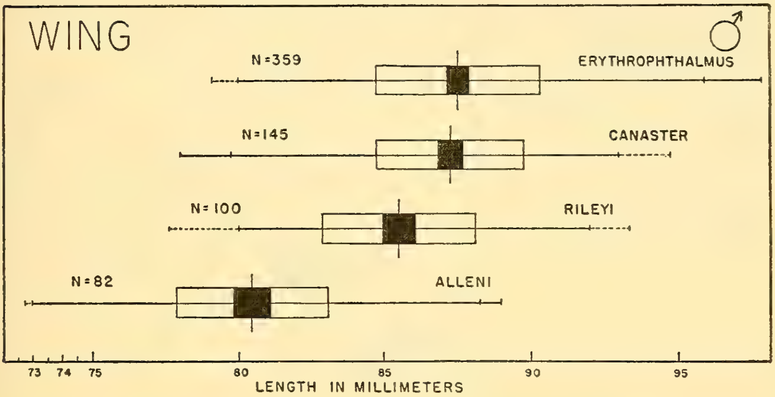

Figure 1. Variation in wing length of males. See page 304 for explanation of figure.

The western sample is significantly different from both the eastern and central samples. Ridgway (1901: 424) comments on variation within this race. He states that birds "from opposite sides of the Alleghenies differ but slightly in average measurements." He gives as substantiating evidence, measurements of 9 adult males from "east of the Alleghenies" — wing 89.92, "8 adult males from Mississippi valley" — wing 89.15. In this connection it is pertinent to note that the present study shows considerable difference in samples taken from the extreme eastern and western portions of the range of this race — enough to allow 75 per cent of the western birds to be distinguished from the eastern birds. This character, however, is of no diagnostic value in separating the central population from either the eastern or western samples.

The wing of *canaster* is not significantly shorter than that of *erythrophthalmus*. The mean length for the wing of *canaster* is 87.30 ± .21 mm.

Rileyi is significantly shorter in wing length than either *canaster* or *erythrophthalmus*. The mean length for the wing is 85.53 ± .26 mm. The difference, however, is not of such magnitude as to allow its use as a diagnostic character.

The wing of *alleni* is much shorter, averaging 80.47 ± .29 mm. Wing length is of value diagnostically, furnishing the following percentages of separation[1] from the various races: from *rileyi*, 83.5 per cent; from *erythrophthalmus*, 91 per cent; and from *canaster*, 91.5 per cent.

The general trend in the variation of wing length is from northwest to southeast, with maximum length occurring in the northwest. The most abrupt change occurs at the junction of *rileyi* and *alleni*.

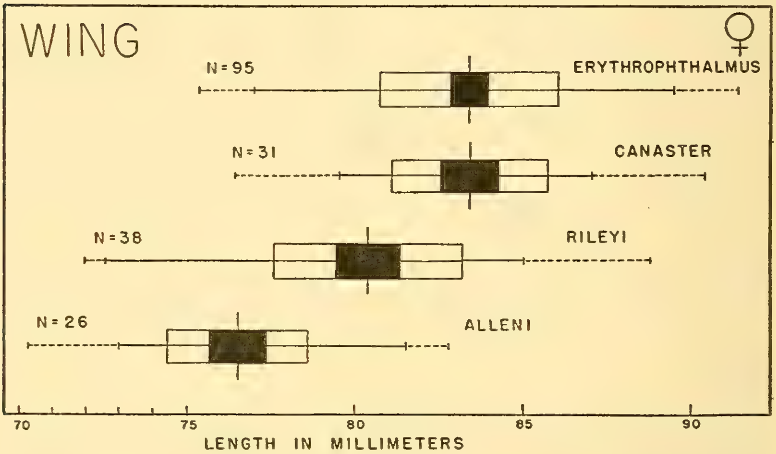

Figure 2. Variation in wing length of females. See page 304 for explanation of figure.

Females (Figure 2). The same pattern of variation observed in the males appears in the females. *Erythrophthalmus* and *canaster* have the longest wings, averaging 83.38 ± .28 and 83.45 ± .42 mm., respectively. The means are not significantly different. The wing in *rileyi* is shorter, 80.32 ± .46 mm., and furnishes 74.8 per cent separation from *canaster*, and 65.7 per cent from *erythrophthalmus*. *Alleni* has the shortest wing, 76.50 ± .47 mm. Separation of 91 per cent from *erythrophthalmus*, 94.2 per cent from *canaster* and 78.3 per cent from *rileyi* is obtained by using this character.

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[1] In comparing the degree of separation of two samples the "per cent separation" was determined by averaging the separate degrees of separation afforded. Thus, if 76 per cent of Form A was separable from 74 per cent of Form B, the "per cent separation" was 75 per cent.

Table 9
P. e. erythrophthalmus
(Sample 1)
Males

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Devi- ation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	211	86.63	.16	2.37	84.26–89.00	80.0– 94.0
Tail	205	92.04	.27	3.83	88.21–95.87	83.0–103.1
Tail Spot	200	36.10	.32	4.58	31.52–40.68	24.0– 55.0
Culmen	206	14.51	.04	.61	13.90–15.13	13.0– 16.0
Mandible Width	201	8.61	.02	.31	8.30– 8.92	7.5– 9.5
Tarsus	208	27.42	.06	.87	26.56–28.29	25.4– 29.5
Middle Toe	205	19.58	.05	.72	18.86–20.30	17.5– 22.0

Table 10
P. e. erythrophthalmus
(Sample 2)
Males

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Devi- ation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	63	87.32	.28	2.21	85.12–89.53	82.1– 93.1
Tail	63	92.70	.43	3.42	89.28–96.11	85.9–103.0
Tail Spot	62	36.85	.61	4.79	32.07–41.64	25.1– 50.2
Culmen	62	14.56	.06	.45	14.11–15.00	13.6– 15.5
Mandible Width	63	8.61	.03	.22	8.39– 8.83	8.1– 9.2
Tarsus	58	27.05	.09	.76	26.29–27.82	24.8– 29.1
Middle Toe	63	19.64	.08	.63	19.01–20.27	18.1– 21.1

Table 11
P. e. erythrophthalmus
(Sample 3)
Males

Measurement	*N*	*Mean*	*Standard Error of Mean*	*Standard Deviation*	*Mean ± Standard Deviation*	*Observed Range*
Wing	85	89.77	.28	2.61	87.16–92.38	84.9– 96.0
Tail	83	96.78	.36	3.05	93.73–99.83	89.1–104.0
Tail Spot	83	38.10	.42	3.82	34.28–41.92	29.1– 50.0
Culmen	84	14.60	.06	.53	14.06–15.13	13.0– 15.9
Mandible Width	82	8.72	.03	.29	8.43– 9.01	8.0– 9.5
Tarsus	84	27.50	.09	.81	26.69–28.30	25.2– 19.5
Middle Toe	83	19.80	.08	.72	19.08–20.51	17.4– 22.4

Table 12
Pipilo erythrophthalmus erythrophthalmus versus *P. e. alleni*, *P. e. canaster* and *P. e. rileyi*

Males	*Vs. alleni*			*Vs. canaster*			*Vs. rileyi*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	1.33	91.0	83.8	X	X	X	Z	Z	Z
Tail	Z	Z	Z	Z	Z	Z	Z	Z	Z
Tail Spot	2.09	97.1	29.0	.57	68.0	34.4	1.62	94.5	30.7
Culmen	Z	Z	Z	.81	79.0	15.0	.96	88.0	15.0
Mandible	Z	Z	Z	Z	Z	Z	Z	Z	Z
Tarsus	Z	Z	Z	Z	Z	Z	Z	Z	Z
Toe	.53	70.0	19.31	Z	Z	Z	Z	Z	Z

Table 13

Pipilo erythrophthalmus erythrophthalmus versus *P. e. canaster, P. e. alleni* and *P. e. rileyi*

Females	*Vs. canaster*			*Vs. alleni*			*Vs. rileyi*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	X	X	X	1.40	92.0	79.6	.53	60.0	81.9
Tail	X	X	X	Z	Z	Z	X	X	X
Tail Spot	.80	79.0	28.8	2.14	93.5	24.0	1.36	92.0	27.3
Culmen	.65	74.5	14.9	Z	Z	Z	.79	79.0	15.1
Mandible	X	X	X	X	X	X	X	X	X
Tarsus	.65	74.5	27.2	Z	Z	Z	Z	Z	Z
Toe	Z	Z	Z	X	X	X	X	X	X

Table 14

Pipilo erythrophthalmus canaster versus *P. e. alleni, P. e. erythrophthalmus* and *P. e. rileyi*

Males	*Vs. alleni*			*Vs. erythrophthalmus*			*Vs. rileyi*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	1.33	91.0	85.0	X	X	X	Z	Z	Z
Tail	Z	Z	Z	Z	Z	Z	X	X	X
Tail Spot	1.33	91.0	25.6	.55	71.0	34.4	.71	76.5	28.2
Culmen	Z	Z	Z	.81	79.5	15.0	X	X	X
Mandible	.68	75.0	8.7	Z	Z	Z	X	X	X
Tarsus	.72	76.5	27.5	Z	Z	Z	X	X	X
Toe	.77	78.0	19.5	Z	Z	Z	Z	Z	Z

Table 15

Pipilo erythrophthalmus canaster versus *P. e. alleni*, *P. e. rileyi* and *P. e. erythrophthalmus*

Females	*Vs. alleni*			*Vs. rileyi*			*Vs. erythrophthalmus*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	1.55	94.0	79.9	.57	75.0	82.1	X	X	X
Tail	.74	77.0	87.9	X	X	X	X	X	X
Tail Spot	1.58	94.0	21.2	.67	75.0	24.6	.76	78.0	28.8
Culmen	Z	Z	Z	X	X	X	.60	72.0	14.9
Mandible	Z	Z	Z	X	X	X	X	X	X
Tarsus	1.05	85.5	26.8	X	X	X	X	X	X
Toe	.73	77.0	19.1	X	X	X	Z	Z	Z

Table 16

Pipilo erythrophthalmus rileyi versus *P. e. alleni*, *P. e. erythrophthalmus* and *P. e. canaster*

Males	*Vs. alleni*			*Vs. erythrophthalmus*			*Vs. canaster*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Di vision Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	.97	83.5	83.0	Z	Z	Z	Z	Z	Z
Tail	Z	Z	Z	Z	Z	Z	X	X	X
Tail Spot	.73	77.0	23.0	1.41	92.0	30.72	.74	78.0	28.2
Culmen	Z	Z	Z	.86	80.5	15.0	X	X	X
Mandible	.60	77.5	8.7	Z	Z	Z	X	X	X
Tarsus	.75	77.5	27.5	Z	Z	Z	X	X	X
Toe	.70	76.0	19.5	Z	Z	Z	Z	Z	Z

Table 17

Pipilo erythrophthalmus rileyi versus *P. e. alleni*, *P. e. canaster* and *P. e. erythrophthalmus*

Females	*Vs. alleni*			*Vs. canaster*			*Vs. erythrophthalmus*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	.81	79.5	78.0	.65	74.5	82.1	.57	71.5	81.9
Tail	.62	73.0	87.4	X	X	X	X	X	X
Tail Spot	1.34	91.0	19.5	.59	72.0	24.6	1.53	94.0	27.3
Culmen	.64	74.0	15.0	X	X	X	.74	77.0	15.1
Mandible	Z	Z	Z	X	X	X	X	X	X
Tarsus	.83	80.0	26.6	X	X	X	Z	Z	Z
Toe	.46	67.5	19.0	X	X	X	X	X	X

Table 18

Pipilo erythrophthalmus alleni versus *P. e. rileyi*, *P. e. erythrophthalmus* and *P. e. canaster*

Males	*Vs. rileyi*			*Vs. erythrophthalmus*			*Vs. canaster*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	.97	83.5	83.0	1.31	91.0	83.8	1.35	92.0	85.0
Tail	Z	Z	Z	Z	Z	Z	Z	Z	Z
Tail Spot	.68	75.5	23.0	1.91	97.1	28.2	1.31	91.0	26.6
Culmen	Z	Z	Z	Z	Z	Z	Z	Z	Z
Mandible	.57	71.0	8.8	Z	Z	Z	.64	74.0	8.7
Tarsus	.76	78.0	27.5	Z	Z	Z	.73	77.0	27.5
Toe	.64	74.0	19.5	.46	67.5	19.3	.78	78.5	19.5

Table 19
Pipilo erythrophthalmus alleni versus *P. e. rileyi*, *P. e. canaster* and *P. e. erythrophthalmus*

Females	*Vs. rileyi*			*Vs. canaster*			*Vs. erythrophthalmus*		
Measurement	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*	d/σ	*Per cent Separation*	*Division Point*
Wing	.74	77.0	78.0	1.62	94.5	79.9	1.51	93.5	79.6
Tail	.59	75.5	87.4	.74	77.0	87.9	Z	Z	Z
Tail Spot	1.26	87.5	19.5	1.60	94.5	21.2	2.39	99.2	24.0
Culmen	.61	73.0	15.0	.40	66.5	14.9	Z	Z	Z
Mandible	Z	Z	Z	Z	Z	Z	X	X	X
Tarsus	.84	80.0	26.6	1.06	85.5	26.8	Z	Z	Z
Toe	.60	77.5	19.0	.68	75.5	19.1	X	X	X

Tail Length

Males (Figure 3). *Canaster* and *rileyi* have the longest tails. *Canaster* averages 94.95 ± .30 mm. and *rileyi* 94.59 ± .36 mm. They are not significantly different in this respect. Both *canaster* and *rileyi* differ

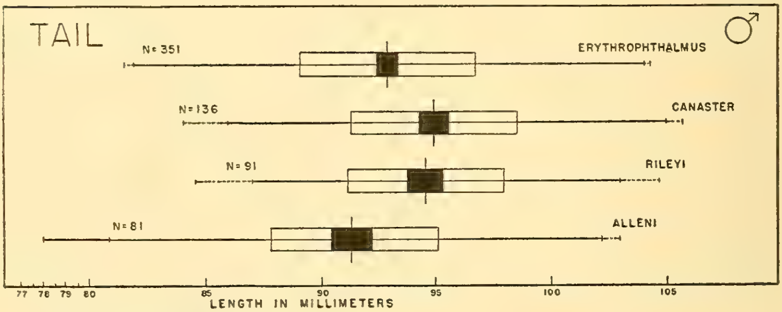

Figure 3. Variation in tail length of males. See page 304 for explanation of figure.

significantly from *erythrophthalmus* and *alleni*. *Erythrophthalmus* has a mean tail length of 92.91 ± .20 and *alleni* 91.43 ± .42 mm.

The trend of geographic variation in wing length within *P. e. erythrophthalmus* is repeated in tail length. The three samples from east to west average respectively, 92.04 ± .27, 92.70 ± .44 and 96.78 ± .36 mm. The western sample is again significantly different from the other two. Ridgway's measurements show the reverse in so far as general trend — nine eastern males 94.74, eight western males 93.73 mm.

Tail length, while of no value as a diagnostic character, shows an interesting pattern of geographic variation: maximum length in the far northwest, next largest in the coastal plains and piedmont areas, smaller again in the north-central and eastern areas, and smallest in peninsular Florida.

Females (Figure 4). *Canaster* and *rileyi* have the longest tails, the former averaging 90.43 ± .62 mm., and the latter 89.70 ± .67 mm. The difference is not statistically significant. The tail in *erythrophthalmus* is not significantly shorter than these, averaging 88.22 ± .41 mm. *Alleni* has a much shorter tail, 85.43 ± .67 mm., and this character serves to separate the Florida race from *rileyi* and *canaster*, with 74.3 per cent and 77 per cent accuracy, respectively. The mean tail length in *alleni*, though significantly different from that of *erythrophthalmus*, furnishes less than 50 per cent separation from this form.

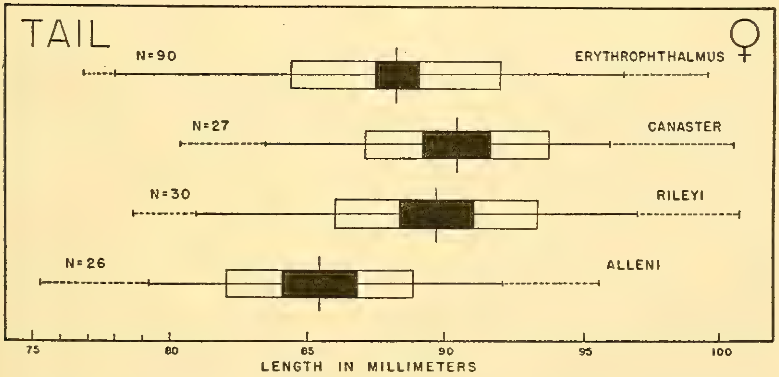

Figure 4. Variation in tail length of females. See page 304 for explanation of figure.

Tail Spot

Males (Figure 5). *Erythrophthalmus* shows the greatest linear extent of white on the outermost rectrix, 36.70 ± .24 mm. The western sample of this population averages 38.10 ± .15 mm., a significant difference from the eastern (36.10 ± .32) but not from the central sample (36.85 ± .61 mm.). Ridgway, in commenting on variation in this character in *P. e. erythrophthalmus,* found the reverse of the results presented here. His nine eastern males and eight western males averaged 40.64 and 38.35 mm., respectively.

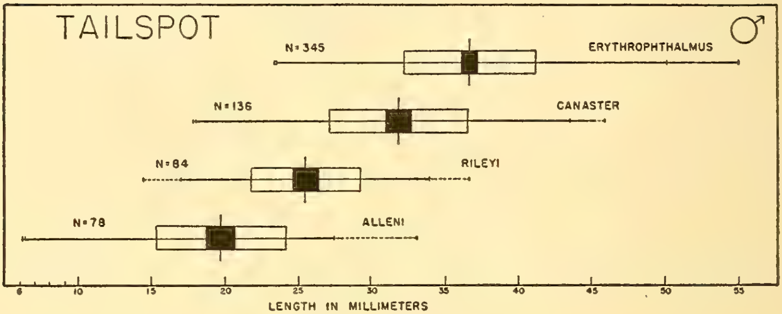

Figure 5. Variation in length of white spot on outermost rectrix of males. See page 304 for explanation of figure.

The tail spot of *canaster* averages 31.79 ± .40 mm., a significant difference from that of *erythrophthalmus.* Howell (1913) used this as a diagnostic character in separating *canaster* from *erythrophthalmus.* However, I find this to be unreliable under statistical scrutiny, since only 69.5 per cent of the *erythrophthalmus* sample is separable from that of *canaster.*

Rileyi has the next smallest amount of white on the tail, averaging 25.50 ± .41 mm. This race shows a significant difference from *erythrophthalmus, canaster* and *alleni.* In my samples *rileyi* shows 77.3 per cent separation from *canaster,* 93.3 per cent from *erythrophthalmus,* and 76.3 per cent from *alleni.* This character is of diagnostic value in separating *rileyi* from *canaster, erythrophthalmus* and *alleni.*

P. e. alleni has the smallest amount of white on the tail, the spot on the outermost rectrix averaging 19.71 ± .50 mm. The difference is statistically significant and allows the use of this measurement for diagnostic purposes. The tail spot of *alleni* affords 97.1 per cent separation from *erythrophthalmus,* 76.3 per cent from *rileyi,* and 90.8 per cent from *canaster.*

The variation in this character shows a northwest-southeast trend, the amount of white diminishing as populations are examined from North Dakota south and east to peninsular Florida. Of interest is the fact that among the Florida material studied, those having the smallest
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amount of white (6–8 mm.) came from coastal localities within the peninsula.

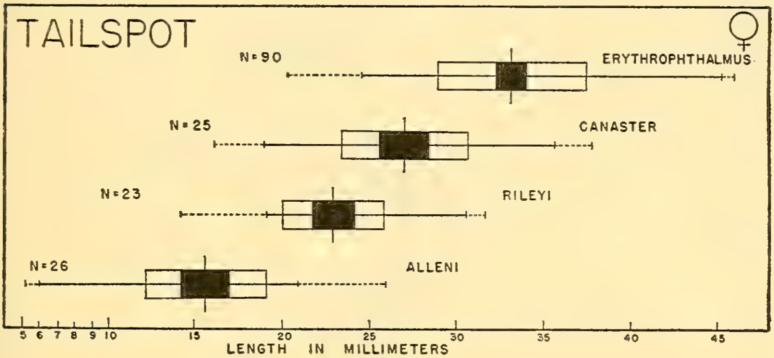

Figure 6. Variation in length of white spot on outermost rectrix of females. See page 304 for explanation of figure.

Females (Figure 6). *P. e. erythrophthalmus* shows the greatest amount of white on the rectrices. The average extent is 33.18 ± .46. This character is of diagnostic value in separating *erythrophthalmus* from *canaster* (78.5 per cent), from *rileyi* (93.0 per cent) and from *alleni* (94.3 per cent). *Canaster* in turn is separable from *rileyi* (73.5 per cent) and from *alleni* (94.3 per cent). *Rileyi-alleni* separation on the basis of this character is 89.3 per cent correct. The females show the same pattern of geographic variation as do the males.

Culmen Length

Males (Figure 7). The length of culmen is quite different in its geographical variation from those characters previously discussed. Howell (1913: 202) first called attention to the longer bill found in the race he designated as *canaster*. In the material examined in this study it was found that the culmen of *canaster* averages 15.44 ± .05 mm. *Erythrophthalmus,* to the north, averages 14.49 ± .03 mm. On the basis of this character 75.3 per cent separation of *erythrophthalmus* from *canaster* obtains.[1]

In the three northern samples (*erythrophthalmus*) no significant difference in culmen length was found. The eastern segment of the

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[1] From a practical standpoint it is unfortunate that the optimum point of division falls at 14.96 mm. The culmen measurement is at best a difficult one to make on a short-, heavy-billed bird such as the towhee. In addition the fact that this point lies near an even millimeter, possibly causing bias in measurement, is not helpful. This does not negate the difference, however, and the culmen length is certainly an indicator of the racial distinctness of this form.

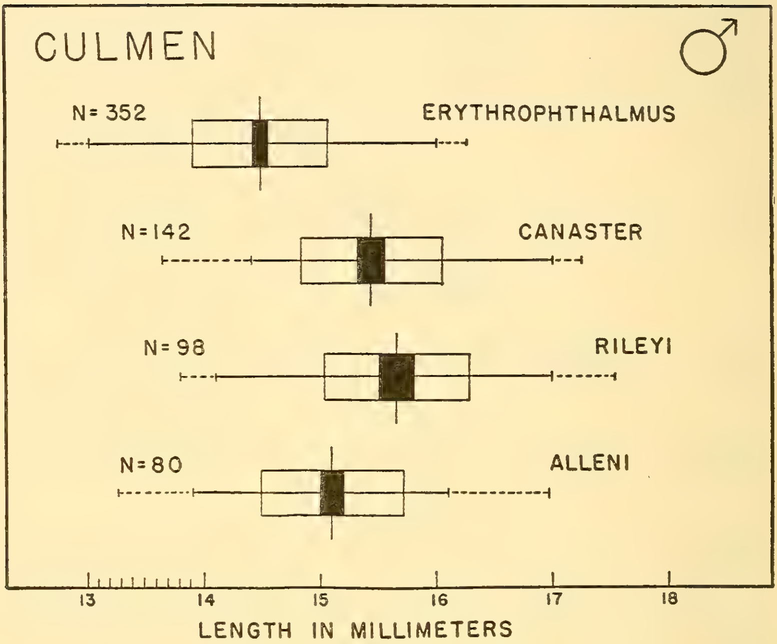

Figure 7. Variation in culmen length of males. See page 304 for explanation of figure.

population averaged 14.51 ± .04, the central segment 14.56 ± .06 and the western segment 14.60 ± .06 mm. Ridgway found a greater difference in the material he had at hand, nine eastern males averaging 14.22 and eight western males averaging 13.97 mm.

The culmen of *rileyi* is significantly longer than that of *canaster*, averaging 15.65 ± .06 mm. The difference is not sufficient to separate *canaster* from *rileyi*. However, 84.3 per cent of *rileyi* and *erythrophthalmus* are separable.

Culmen length in *alleni* is significantly less than that of *canaster* and *rileyi*, the average length being 15.05 ± .07 mm. Although serving to indicate a difference in the population, it is not of diagnostic value.

Maximum culmen length is obtained in *canaster* and *rileyi*. To the north and south it diminishes, and the northwest-southeast trend is not as pronounced as in other characters.

Females (Figure 8). *P. e. canaster* and *rileyi* females have the longest culmens, averaging 15.20 ± .10 mm. and 15.34 ± .09 mm., respectively. *Canaster* is separable with 73.5 per cent accuracy from

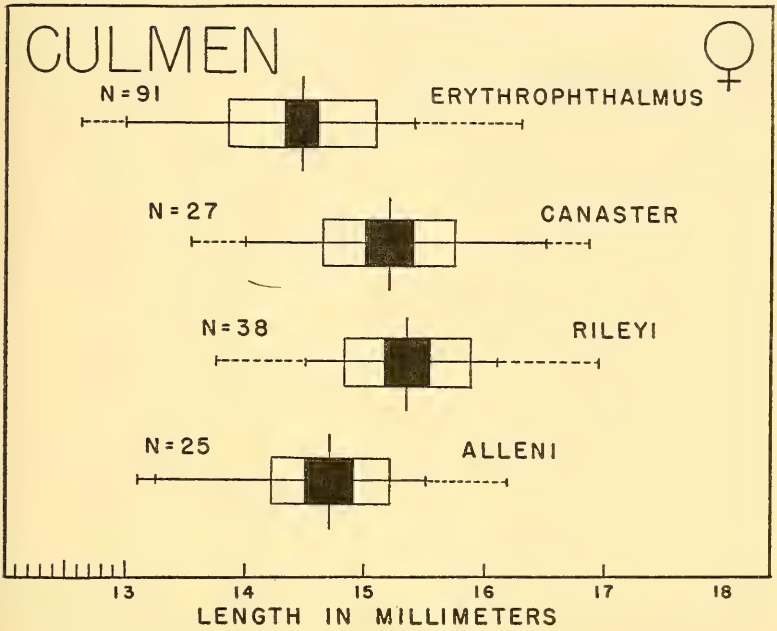

Figure 8. Variation in culmen length of females. See page 304 for explanation of figure.

erythrophthalmus, which averages 14.47 ± .07 mm. Correct identification of *erythrophthalmus* and *rileyi* obtains 78.0 per cent of the time. *Alleni,* averaging 14.71 ± .10 mm., is significantly smaller than *erythrophthalmus, canaster* and *rileyi.* The degree of separation of *alleni* from the other three races is less, however, than 75.0 per cent. The pattern of geographic variation in the females is the same as in the males.

Width of Lower Mandible

Males (Figure 9). Lower mandible width shows much the same geographic variation as does culmen length. *Canaster* has the widest bill, with a mean of 8.94 ± .03 mm. It is significantly different from *erythrophthalmus* in this measurement, the average width in the latter being 8.68 ± .02 mm. Within the northern race the western birds appear to have a slightly larger bill, with a mean of 8.72 ± .03 mm. This is near the borderline of significance in relation to the eastern birds, with a mean of 8.61 ± .02 mm. The material examined from the northcentral area has a mean mandible width of 8.61 ± .03 mm.

It shows no significant difference from the adjacent segments to the east and west.

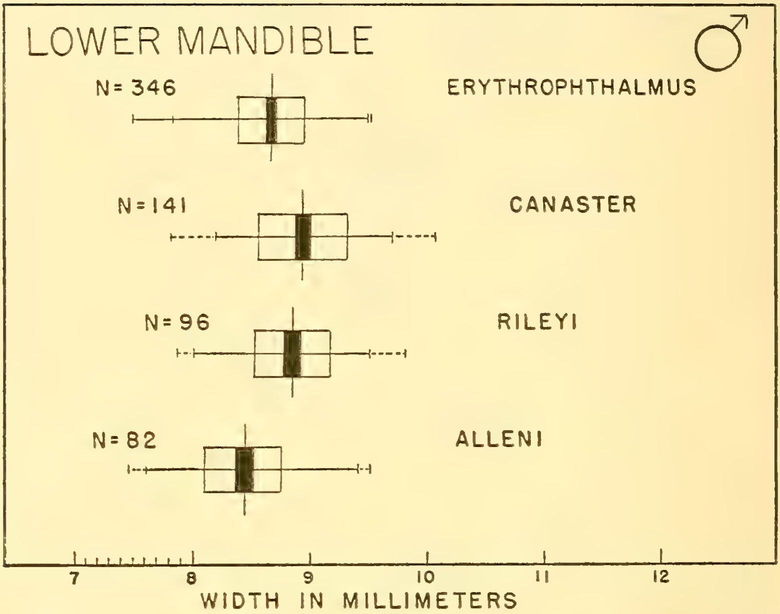

Figure 9. Variation in width of lower mandible of males. See page 304 for explanation of figure.

The bill of *rileyi* has a mean width of 8.85 ± .03 mm., which is not significantly different from that of *canaster*. It is, however, significantly different from *erythrophthalmus*. *Rileyi* is separated from *alleni* 74.3 per cent of the time.

Alleni has a smaller bill, averaging 8.48 ± .04 mm. A significant difference is shown in relation to *canaster* and *rileyi*. *Alleni* is separable from *canaster* 74.5 per cent of the time.

Of interest is the fact that *erythrophthalmus* and *alleni* show no difference in this character. Once again a northwest-southeast gradient is present, with maximum size in *canaster* and *rileyi*.

Females (Figure 10). The width of the lower mandible is of no diagnostic value in this sex. *Canaster* and *rileyi* have the greatest average width, 8.69 ± .05 and 8.79 ± .07 mm., respectively. They are not significantly different in this character. *Erythrophthalmus* averages slightly smaller (8.60 ± .04 mm) but is not significantly different from *canaster* and *rileyi*. *Alleni* is significantly smaller than

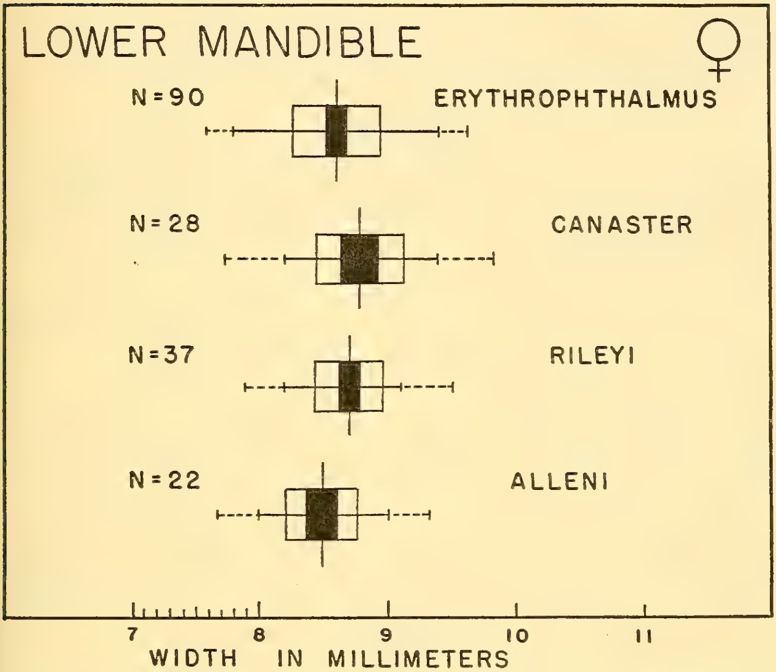

Figure 10. Variation in width of lower mandible of females. See page 304 for explanation of figure.

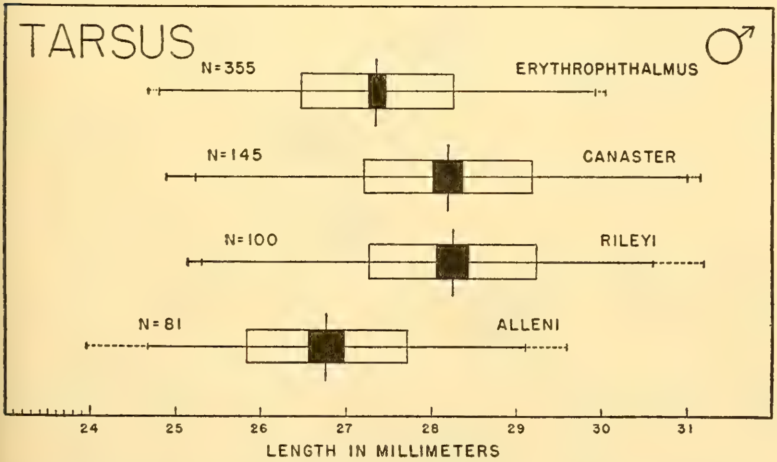

Figure 11. Variation in length of tarsus of males. See page 304 for explanation of figure.

rileyi and *canaster,* averaging 8.47 ± .06 mm. *Alleni* and *erythrophthalmus* are not significantly different from each other.

Tarsus Length

Males (Figure 11). The length of tarsus shows much the same geographic trend of variation as do the characters previously discussed. *Rileyi* and *canaster* have the longest tarsi, 28.25 ± .10 and 28.19 ± .08 mm., respectively. The difference is not statistically significant in this case.

Erythrophthalmus has a shorter tarsus, averaging 27.37 ± .05 mm. Although the tarsus is significantly different from that of *canaster, rileyi* and *alleni,* the character is of no diagnostic value.

Alleni has the shortest tarsus, average length being 26.78 ± .11 mm. Tarsus length is of diagnostic value in separating *alleni* from *canaster* and *rileyi.* In *canaster-alleni* separation, 76.8 per cent correctness of identification is achieved, and in *rileyi-alleni* 77.3 per cent.

Within the population here considered as *erythrophthalmus* I find no significant difference in the three samples studied. The eastern sample averages 27.42 ± .06, the central sample 27.05 ± .01, and the western sample 27.50 ± .09 mm. Ridgway obtained the same results in his earlier study, the nine eastern and eight western males each averaging 28.45 mm.

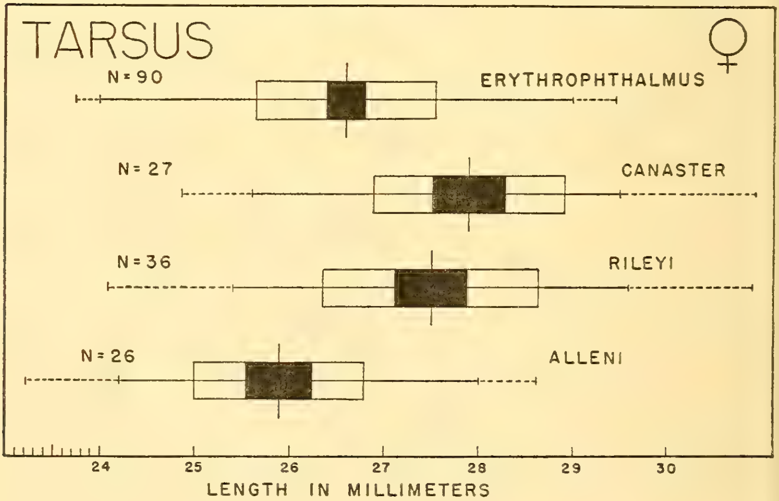

Figure 12. Variation in length of tarsus of females. See page 304 for explanation of figure.

Females (Figure 12). *Alleni* has the shortest tarsus, averaging 25.89 ± .18 mm. It is significantly different from *erythrophthalmus,* which averages 26.60 ± .10 mm. *Alleni* is 80.0 per cent separable from *rileyi,* whose tarsus averages 27.54 ± .19 mm. There is 85.5 per cent separation of *alleni* from *canaster,* whose tarsus averages 27.91 ± .20. *Canaster* and *rileyi* are not significantly different from each other in this character. *Erythrophthalmus* and *canaster* are 75.5 per cent separable. Less than 50 per cent separation obtains in *rileyi-erythrophthalmus* samples. The pattern of geographic variation is the same as that found in the males.

Middle Toe Without Claw

Males (Figure 13). *Canaster,* with a mean middle toe length of 20.19 ± .07 mm., has the longest toe, and is significantly different from *erythrophthalmus, rileyi* and *alleni* in this measurement. Nevertheless, only in the case of *alleni* and *canaster* is this character of diagnostic value, furnishing 78.3 per cent correct identification.

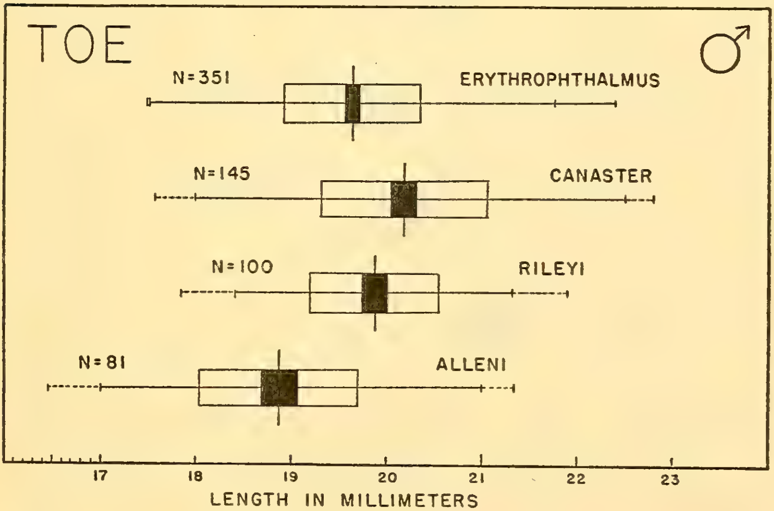

Figure 13. Variation in length of middle toe without claw of males. See page 304 for explanation of figure.

Rileyi has the next smallest middle toe, averaging 19.89 ± .07 mm. As pointed out above, it is significantly different from *canaster* in this measurement. In addition it is significantly different from *alleni* to the south and from *erythrophthalmus* to the north.

The toe of *erythrophthalmus* averages 19.64 ± .04 mm. This is significantly shorter than that found in *canaster* and *rileyi*, and significantly longer than that found in *alleni*. No significant difference was found in the samples examined from the eastern, central and western portions of the range of *erythrophthalmus*. Ridgway found that there was little difference in his nine eastern and eight western males. The average middle toe measurement was 19.81 and 19.56 mm., respectively.

Alleni has a much shorter toe than any of the other races, averaging 18.88 ± .09 mm. On the basis of this measurement *alleni* is separable from *canaster* in 78.3 per cent of the material examined. It is also separable in 75.0 per cent of the cases from *rileyi*. Correct separation from *erythrophthalmus* is possible in less than 70 per cent of a mixed sample of the two populations.

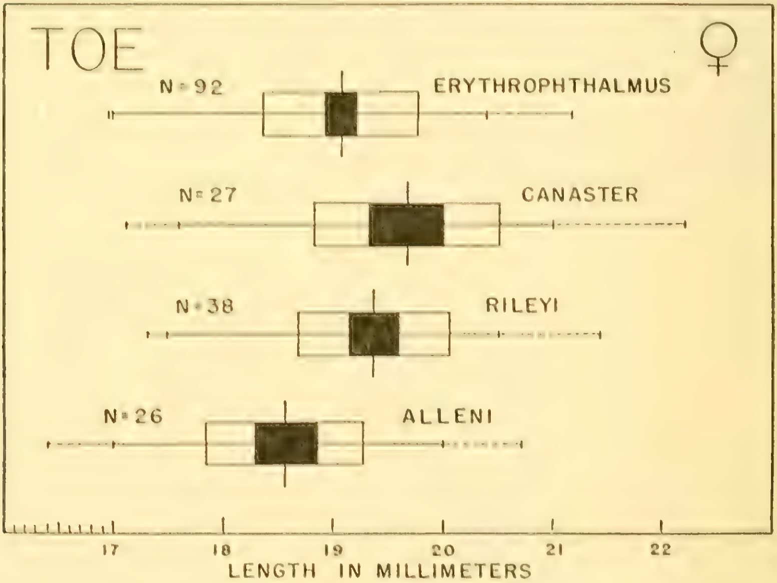

Figure 14. Variation in length of middle toe without claw of females. See page 304 for explanation of figure.

A general northwest-southeast clinal trend is observable in this character as in the others already discussed — maximum size occurring once again in *canaster* and *rileyi*, with diminishing size to the northwest and southeast.

Females (Figure 14). The middle toe in the female is not as variable as in the male, although the same pattern of geographic variation appears. *Canaster* and *rileyi*, not differing significantly from each other, have the longest middle toes, averaging 19.66 ± .16 and 19.38 ± .11 mm., respectively. *Canaster* is significantly different from *erythrophthalmus*, which averages 19.06 ± .08 mm., and from *alleni*, which averages 18.57 ± .14 mm. Accuracy of 76.3 per cent is attained in separation of *canaster* from *alleni*. *Rileyi* is significantly different from *alleni*, but not from *erythrophthalmus* in this measurement.

Tail Spot: Tail

Males (Figure 15, upper). The ratio of extent of white on the outermost rectrix to length of tail proves to be of value in separating *erythrophthalmus* and *canaster*. In these two races the tail length and tail spot vary reciprocally, and for this reason the differences are magnified by calculation of this simple ratio. In *erythrophthalmus*, the tail spot is 39.36 ± .27 per cent of the tail length, and in *canaster* the percentage is 32.59 ± .45. This furnishes 74.5 per cent separation of these two forms.

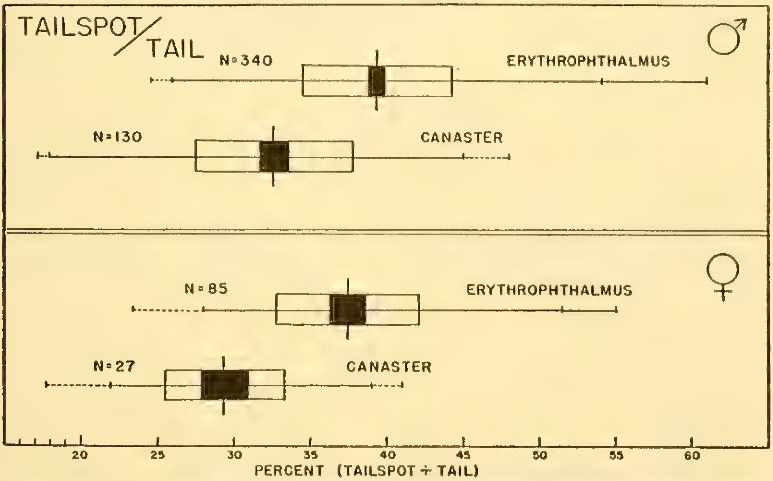

Figure 15. Variation in length of white spot on outermost rectrix: males (upper) and females (lower). See page 304 for explanation of figure.

Females (Figure 15, lower). In the females *P. e. canaster* has a mean of 29.41 ± .74 per cent, and *erythrophthalmus* a mean of 37.47 ± .51 per cent. The disproportionate increase in length of tail spot to length of tail makes for an even greater divergence in this sex, with 82.3 per cent separation obtaining.

Number of Rectrices Showing White on the Inner Web

Males and Females (Table 20). The greater extent of white on the inner web of the outermost rectrix in the northern races has been commented on earlier. In addition to extent of white it is also true that more individual rectrices show white in the northern population. The males in *P. e. erythrophthalmus* furnish the upper extreme, occasionally showing white on as many as five pairs of feathers. One female of *alleni* showed white on only a single pair. In general males tend to show white on more feathers than do females. The character is of little diagnostic value in relation to the populations but may prove helpful in individual identifications. Table 20 presents the data for this character.

Table 20
Variation of White on Rectrices
Number of pairs involved, expressed in per cent of total sample

Subspecies		*Pairs of Rectrices with White*				
		1	*2*	*3*	*4*	*5*
MALES	*erythrophthalmus* (N = 347)		0.6	43.8	52.7	2.9
	canaster (N = 143)		2.1	75.5	22.4	
	rileyi (N = 97)		7.6	87.0	5.4	
	alleni (N = 79)		32.9	59.5	7.6	
FEMALES	*erythrophthalmus* (N = 89)		1.1	69.7	29.2	
	canaster (N = 25)		12.0	80.0	8.0	
	rileyi (N = 24)		20.0	79.2		
	alleni (N = 24)	4.2	75.0	20.8		

Iris Color

Males and Females. Variation in iris color presents some difficulty in analysis for the reasons outlined in the introduction of the present paper. *P. e. erythrophthalmus* and *P. e. alleni* may be largely disregarded, since they uniformly have "red" and "white" irides, respectively. *Canaster* and *rileyi,* on the other hand, show mixtures in varying degrees of these two basic colors, and it appears that a knowledge of variation in iris color is quite important in gaining a clearer understanding of the racial relationships within the species.

Basically it is readily apparent that the intermediate eye colors are found in the areas of geographic intermediacy between the northern and southern races (Map 3). The map does not attempt to weigh the different iris colors according to relative percentages but simply furnishes a record of the limits of distribution of the three colors plotted. Arbitrary classification of the multiplicity of color notations made by various collectors was quite necessary. An attempt was made to be as conservative as possible in the interpretation of the color notation made on the labels. Weighing of the several colors was accomplished by use of the Chi-square test (Table 21). The degree of association of iris color with geographic locality is very high, so high that it may safely be assumed that the probability of such distribution occurring by chance alone is nil.

Iris color in *canaster* may be "orange" or "yellow" but it is usually red (84.25 per cent). In *rileyi* the color may be "red" or "orange" but it is usually yellow (79 per cent).

Material from the type localities is unfortunately slightly confusing. A *canaster* topotype (JCD 269) taken near Mobile, Alabama, had yellowish irides. Specimens (PB 15771 and JCD 263) taken by Dr. Pierce Brodkorb and myself near Brunswick, Georgia, were close to salmon (10-G-3) and buff (10-I-5), respectively.

There seems to be no reason to call upon any genetic principle more complicated than multiple factors or multiple allels for explanation of this distribution. No clues are available at present to indicate the number of genes involved, but the almost perfect blending of pigments seems to follow the pattern usually associated with these types of inheritance. The splotchy distribution of color found in some individuals, and reports of pie-shaped segments of different colors in the irides furnish further support for this hypothesis.

The iris color in juvenals has apparently been overlooked by most investigators dealing with the pale-eyed birds of the southeast. Maynard (1881: 114) states that Florida nestlings have light brown irides. The young birds of the north have iris color that is usually described as "muddy brown", "brownish", "sepia-brown", "dark

Table 21

Variation in Iris Color

The Alabama, Mississippi, Louisiana, west Florida and central Georgia records represent *P. e. canaster.*

The coastal North Carolina, coastal South Carolina and southeastern Georgia records represent *P. e. rileyi.*

		IRIS COLOR		
	MALES	RED	ORANGE	YELLOW
LOCALITY	Ala., Miss., La., west Fla., central Georgia	119	19	4
	Coastal N. C., S. C., southeast Georgia	2	12	59

$\chi^2 = 158.54$ (Surely significant)

		IRIS COLOR		
	MALES	RED	ORANGE	YELLOW
LOCALITY	Ala., Miss., La., west Fla., central Georgia	20	3	0
	Coastal N. C., S. C., southeast Georgia	0	7	20

$\chi^2 = 41.52$ (Surely significant)

		IRIS COLOR		
	BOTH SEXES	RED	ORANGE	YELLOW
LOCALITY	Ala., Miss., La., west Fla., central Georgia	139	22	4
	Coastal N. C., S. C., southeast Georgia	2	19	79

$\chi^2 = 190.67$ (Surely significant)

brown", "brown", or some other color designation which appears to fall in the brown category. Sutton (1935: pl. III) pictures a 15-day old male bird from Michigan as having dark brown irides. Fully-fledged juvenals (JCD 180) taken in Florida, and in Georgia, 5 miles north of Brunswick, Glynn County, (JCD 260 and 264) have the iris color near "Pale Neutral Gray" in Ridgway's system and 15-A-3 in Maerz and Paul.

Plumage Characteristics of Females

Efforts to establish color classes for the various parts of the plumage were not successful. The range and variability of the colors is such that clear-cut differences are not observed. Four areas of plumage were scrutinized: back, flanks, breast and crown. After it was decided that it was not possible to use the techniques of color classes for statistical analyses of the plumage characters, the material was identified on the basis of mensural characters and notations made as to range of color in the various races.

The possibility of color change due to age of skins was considered, and old skins (1930 and earlier) were compared with fresh material (1940 and later). I was not able to detect any change due to museum age.

Back color. P. e. erythrophthalmus as a whole is more reddish brown than *P. e. alleni* and *P. e. rileyi*. Some skins (CM 2290) are quite reddish (15-A-12); others (USNM 363240) though reddish are very pale, (15-H-9). USNM 23598 is much darker (15-H-9) than the average. USNM 56535 is dark but not quite as reddish (8-H-12). The average color of this race appears to be best represented by UMMZ 96950, (15-J-8). Birds in fresh plumage are slightly darker than those showing wear, and a skin from Jackson County, Michigan (GMS, Oct. 11, 1949), is typical of these fresh-plumaged birds (8-E-11).

In *P. e. rileyi* the older skins show more red pigment than the fresh material. In this case, however, the older material is from the northern and inland localities where *rileyi* meets *canaster* and *erythrophthalmus*, both of which are on the average more reddish than *rileyi*. MCZ 208060 is typical (15-C-11). In this case it seems quite likely that the difference is due to geographic rather than temporal factors. The coastal localities provide material that is very similar to *alleni* in general color (15-E-7). Some individuals are much darker (JCD 258 and PB 15772).

The *canaster* sample shows no detectable differences due to age of skins. USNM 38247 (1946) matches CNHM 166708 (1916) in back color (15-E-11). The average color of the sample is typified by USNM

340494 (15-E-9). The material examined appears to be more olive and reddish than the *alleni* sample and slightly grayer than *erythrophthalmus.*

Alleni is conspicuously grayer than *erythrophthalmus* and *canaster* but not grayer than *rileyi.* Some individuals, AMNH 368079 (15-J-11), approach *canaster* in redness, but the general color of the sample is typified by USNM 261709 (15-E-7). There is no detectable change in color due to age of skin.

The color of the back does not show any sharp breaks which are correlated with geographic distribution. The northern race shows much more red pigment than the peninsular Florida population, but in the intervening populations the colors are apparently the result of varying admixtures of these extremes.

Flanks. P. e. erythrophthalmus has darker flanks on the average than have the other races. Average color is represented by USNM 339625, 257922 and CM 2762 (13-H-12). Some skins are much darker (14-E-12) than the average, as in USNM 268666, 235598, 306445 and UMMZ 66998. The lightest flanks (13-J-10) in the sample at hand are from a skin taken at Wheeling, West Virginia, on May 2, 1936, now in the M. M. Peet collection.

P. e. rileyi has very uniform coloration of the flanks and is quite like *erythrophthalmus* in color. The darkest specimen (MCZ 10355) is 14-I-11, the lightest (USNM 298673) is 13-K-11, and the average color, as represented by USNM 382391, is 14-C-12.

P. e. canaster is more variable in flank color. The darkest specimen, USNM 382361, is 14-E-12, and the lightest is 13-K-9. The average color is lighter than *erythrophthalmus* and slightly darker than *rileyi.* It is represented by 13-K-9, as found in USNM 378909.

P. e. alleni has much lighter flanks than the other races. USNM 261711, with 13-D-11 flanks, is considered as being typical. The darkest color present in my material is 13-G-10 (USNM 133091). The lightest, 12-I-10, is found in LSU 8148.

Breast. P. e. erythrophthalmus is quite variable in the coloration of this area of plumage. Skins from the far northwest, Grafton, North Dakota, are very dark, 15-C-12, as seen in UMMZ 66998 and 56535. The lightest breast in this sample, 14-H-9, is found in USNM 348791. Some are quite reddish, 15-A-12, USNM 306445. The average color appears to be 14-K-9, as found in AMNH 367858.

P. e. rileyi has more gray pigment (or less red) than *erythrophthalmus.* The grayest, 15-A-6, is JCD 259, while the most reddish, 15-C-11, is found in MCZ 208060. The average color is best represented in MCZ 212455, as 15-C-9.

P. e. alleni shows considerable variation in breast color. The average, 14-J-9, found in USNM 300219, is paler and less red than *rileyi* and *canaster*. JCD 176 is as reddish as the average *canaster* color, 15-C-12. USNM 261711 is the darkest in this sample, 15-C-6, and LSU 8148 is the lightest.

Crown. P. e. erythrophthalmus has the darkest crown of the four races. USNM 338022 and UMMZ 56535 are very dark, 8-E-12. UMMZ 74532 is the lightest, 14-E-8. Some skins show considerable redness, as in CM 2290, which is 15-A-12. GMS 8917 appears to be representative of the average color, 8-L-12.

Canaster is paler than *erythrophthalmus*; the average color, found in USNM 258980, is 7-A-12. One skin, USNM 379723, is very dark, 8-H-12. The lightest color observed, 15-C-12, occurs in a specimen taken in Fulton Co., Georgia, May 2, 1928 (M. M. Peet collection).

P. e. rileyi is slightly paler on the top of the head than is *canaster*. An average skin is represented by USNM 298673, 8-H-11. MCZ 208060 (see breast) is the most reddish, 7-A-12. PB 15772 is the darkest, 8-J-12. AMNH 55406 is very light, 14-L-10.

Alleni is the palest of the four races. The average color, 15-E-12, is present in USNM 261708. JCD 176 (see breast) is quite reddish, 14-C-12. The darkest specimen, AMNH 368317, is 8-H-12.

Summary. There appears to be a general intensification of red and black pigments in the northern areas in all the feathers showing color. There is considerable difference between *erythrophthalmus* and *alleni*, but in so far as I am able to determine, the blending of colors is so gradual and variability is so excessive that coloration is of taxonomic value in this species only when large series are available for comparison.

Plumage Characteristics of Males

Back, Crown and *Breast.* The color of these areas of plumage varies little in the four races. The average color of the back in *erythrophthalmus* is Sooty Black[1]. *Canaster* averages slightly paler, Olivaceous Black (3). Olivaceous Black appears to represent the average color in *rileyi*. *Alleni* is conspicuously paler, Iron Gray. In all of the races there is considerable individual variation, and Sooty Black individuals occur in all four. As a result of wear and bleaching, the darker races occasionally show very pale back colors. The color of the crown and breast presents the same pattern of geographic variation as does the back. To my eye the color of these areas is the same as that of the back.

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[1] Colors approaching black are not adequately treated in Maerz and Paul, and Ridgway (1912) was used for these colors.

Flanks. P. e. erythrophthalmus has the richest color in the flank feathers. The darkest specimen examined was CM 2831, which was 6-A-12. CM 7576 was the lightest of the northern birds, 12-D-11. The average color was matched by 5-D-12 in AMNH 367998.

Canaster is slightly paler than *erythrophthalmus,* darker than *alleni,* and paler than *rileyi.* The darkest specimen, USNM 378920, was 13-K-11. The average color present in this race is 13-D-11, as found in USNM 338901. Some birds are quite light, as light as average *alleni* specimens. The lightest, 12-F-10, was found in USNM 240167.

Rileyi shows little variation in flank color. In a series of eight birds from the type locality seven are remarkably uniform. One (JCD 256) is as dark as the darkest specimen of *P. e. erythrophthalmus,* 6-A-12. The average color is near 13-C-12, as in JCD 253. The palest specimen, JCD 255, is 12-H-8.

The palest of the races, *alleni,* has an average flank color which is near 12-F-10, as present in JCD 178. In the only cotype of this race available to me, MCZ 10721, the color is 12-G-10. JCD 249 is the palest specimen examined and is near 11-H-8. The darkest flanks were found in JCD 178, 13-A-12.

Summary. In this sex the same general intensification of color occurs in the northern races. *Alleni* is conspicuously paler in all plumage showing color. *Rileyi* and *canaster* are intermediate in color. The sample representing *canaster* shows much greater variation than does that of *rileyi.*

NON-GEOGRAPHIC VARIATION

The most unusual individual variant was discovered in a bird of the year taken by W. H. Osgood. The bird was collected in Maryland, 10 miles north of Washington, D. C., on August 1, 1897, and is now No. 367895 in the collection of the American Museum of Natural History. The specimen is labeled as a male, and the greater part of its plumage is clearly of this sex. A large patch of female plumage, however, is present on the upper back, extending forward to the neck and around the right side. No flight feathers appear to be involved. Heterosexual plumage changes have been recorded on many occasions in domestic birds, and Brodkorb (1935) reports what may have been a similar situation in *Falco sparverius.* His explanation of that case as gynandromorphism does not furnish an adequate solution for the pattern present in this case. I am inclined to believe that a non-bilateral pattern is the result of somatic change rather than hormone interplay. In this case there is no information available concerning the gonads, but it does not seem likely that such a spotted distribution would be produced in a sexually dimorphic character by lack of balance in the male and female hormones.

If it is assumed that the towhee has the same type of sex determination as poultry, then another proposal can be made. If this specimen developed from a fertilized ovum carrying a pair of X chromosomes, as such it was destined under normal circumstances to become a male. Distortion of the normal mitotic processes on many occasions has been known to result in the deletion of parts of or whole chromosomes. The number of daughter cells showing the effects of the deletion is dependent upon the stage of development of the individual at the time the aberration occurs. Development of female secondary sex characters from the heteroploid cells, produced in such fashion, is due to the absence of the X chromosome rather than the presence of the Y. Such a chain of events appears to have occurred in this individual.

White-tipped feathers at the bend of the wing, involving the tips of the secondary coverts, and varying degrees of white streaking in the scapulars have long caused speculation as to the affinities of *P. erythrophthalmus* and *P. maculatus* (Baird, Brewer and Ridgway 1874, Allen 1878, Coues 1878, and more recently by Sibley 1950.) The appearance of white at the above mentioned points has been looked upon as evidence of an exchange of germ plasm between the eastern and western species, or as an indicator of common origin of the two forms.

There seems to be some evidence that such an exchange does at least have the opportunity to occur in that the ranges of the two forms closely approach each other. In the breeding material examined in the course of the present study varying degrees of white tipping of the secondary coverts was found in 136 male and 29 female specimens, taken over the entire range of the eastern forms, even in Florida and New York. USNM 302208, a male taken near Athens, Georgia, on February 24, 1930, shows this spotting and streaking of the coverts and scapulars to a marked degree. The iris color, as recorded by T. D. Burleigh, was "dirty yellow." This would seem to rule out the possibility that the bird was a stray from the west.

On the basis of mensural characters the Georgia bird is identified as *P. e. canaster*. The degree of marking is equal to that found in GMS 10172, a male taken at Lincoln, Nebraska, on May 13, 1946. George M. Sutton, the collector, comments on the label "white on back reduced — *P. m. arcticus* approaching *P. e. erythrophthalmus*."

The recommendation made by Sibley (*op. cit.*) that *erythrophthalmus* and *maculatus* be considered conspecific would seem to be a wise action. Although I did not have sufficient material at hand to critically analyze the geographic distribution of this variation I am inclined to think that it is indicative of common origin rather than interbreeding in recent time.

Albinism is quite rare in the species. Only one specimen, an adult female *P. e. erythrophthalmus* from North Carolina, AMNH 104434, shows any appreciable degree of this plumage change. The iris color was recorded as "pearl gray." The pattern of white is bilaterally symmetrical and extends from the front to the rectrices. The neck is white, and the contour feathers of the body are generously sprinkled with white. Several of the primaries and secondaries are involved. Twenty-one other specimens were found showing from one to perhaps several hundred randomly placed white feathers.

In both sexes there is a variation which involves the tips of the crown feathers. In seven specimens from scattered localities these feathers were conspicuously tipped with rufous. This variation may be still another indication of the affinity that exists between the eastern and western segments of the populations. The pattern presented by this variant is similar to that found by Sibley in the hybrid population of Cerro Viejo, Jalisco. (See his plate 12, MVZ numbers 115243 and 115215).

MIGRATORY BEHAVIOR

It has long been known that *P. e. erythrophthalmus* moves well southward during the winter. The practicality of distinguishing red-eyed from pale-eyed individuals in the field has had two effects: (1) to confuse the literature with numerous sight records of this race when the birds may have been *P. e. canaster* and (2) to allow the retention of Howell's original concept of the sedentary nature of *canaster*. It is felt that on the basis of the present study, valid criteria for the identification of the four races have been determined. On the basis of these criteria, wintering material has been examined and identified with interesting results. Admittedly some of the individual identifications are not correct. However, it is assumed that sufficient numbers of specimens were at hand to minimize the danger of false conclusions with reference to the general winter behavior of the four races.

Map 4 shows the result, in summary form, of this phase of the investigation.

P. e. erythrophthalmus withdraws practically all of its numbers from the breeding grounds. Some few individuals for unknown reasons do remain in the northern United States during the winter, but the majority leave, spreading south and west as far as Nueces and Lee Counties, Texas, and south and east in Florida as far as Hillsborough, Okeechobee and Volusia Counties.

P. e. canaster, regarded by Howell as remaining on the breeding grounds during the winter, certainly does this, in so far as a portion of the population is concerned. On the other hand, winter specimens, taken in Florida as far south as Wakulla County on the northern Gulf Coast, indicate some post-breeding movement of individuals. In the material examined there were no specimens of *canaster* from the east coast of Florida. There are numerous winter-taken individuals of *canaster* from south-central Georgia, in the area occupied by *rileyi* during the breeding season. There appears to be a slight retreating of the population along the northern extent of its breeding range. Winter specimens, with one exception, from southern Tennessee, northern Alabama, Mississippi and Louisiana are typical of *erythrophthalmus*.

P. e. rileyi spreads north, south and west, during the winter. The wandering to the north and west is not marked, but to the south *rileyi* extends its population to mid-peninsular Florida. Winter specimens of this race are available from as far south as Charlotte County on the west coast and Brevard County on the east coast. It is apparent, however, that many of the birds do remain within the breeding range outlined for this form. It is interesting to note that the series of cotypes established by Coues' action in describing the Florida race contains some four individuals (C. J. Maynard 2559, 2669, 2592, 2513) whose wing measurements as given indicate that they may have been wintering birds from the north (*rileyi*). This series was taken during February and March. Only one specimen of this series (MCZ 10721) was available to me, and it is typical of *alleni*. My measurement of 77.0 mm. for length of wing as compared with 2.92 inches [74.2 mm.] as given by Allen (1871) probably indicates that these earlier wing length figures represent "chord" measures.[1]

P. e. alleni apparently is largely sedentary. Howell (1932: 448) did not have records available for breeding birds in the extreme southern part of peninsular Florida but did indicate that *alleni* spread southward during the winter to this area. Summer specimens (JCD 185, UMMZ 114394 from southern Dade County, Florida) furnish evidence that this form now extends into the extreme southern tip of Florida as a breeding bird as well as in winter. JCD 185 was taken while in company with females and juvenals. There is no evidence of any extensive post-breeding northward wandering in this race.

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[1] Two discrepancies in the table of measurements given by Allen are worthy of note. A wing length of 3.90 inches (99.1 mm.) for MCZ 10726 must be due to error in measuring or in publication. This length far exceeds any seen by me in any of the four races. There is duplication of MCZ 10729 in having this number assigned to two of Maynard's skins, 2668 and 2669.

VARIATION IN RELATION TO ENVIRONMENT

Ecological Rules

The data available have been examined from the standpoint of several pertinent ecological rules suggested as being applicable to warm-blooded vertebrates. Mayr (1942: 88–92) has summarized these rules and his wording of them is followed below.

Bergmann's Rule. "The smaller-sized races of a species are found in the warmer parts of the range, the larger-sized races in the cooler districts." Insufficient data concerning body weight were available, and hence this measure of size could not be examined adequately. Other measures, wing, tail, culmen, width of lower mandible, tarsus and middle toe, which may possibly be indicators of total body size[1], present a puzzling picture. *Alleni* is smaller than any of the other races in respect to these characters. In keeping with Bergmann's Rule the adjacent races to the north, *canaster* and *rileyi*, are larger. *Erythrophthalmus* from still further north however, is smaller than the intermediate races, though not as small as *alleni*. It is of course difficult to estimate the selective effect of lowered winter temperatures on migratory forms. *Erythrophthalmus* moves well down into those areas where a large portion of *canaster* remains as a resident form during the winter, and for the most part does not experience lower temperatures than the resident southern individuals. A segment of the population of *rileyi* accomplishes this same movement in relation to *alleni* and as a population is probably not subjected to much lower temperature than the peninsular Florida race.

In this case, then, it appears that if the breeding ranges are considered, *alleni* follows the rule in relation to *canaster*, *rileyi* and *erythrophthalmus*. *Canaster* and *rileyi*, however, do not seem to follow the rule in relation to *erythrophthalmus*.

Allen's Rule. "Protruding body parts, such as tails, ears, bills, extremities, and so forth, are relatively shorter in the cooler parts of the range of the species than in the warmer parts." Lack of information concerning total body size made valuation of this rule difficult. Examination of culmen length, mandible width, tarsus and toe, however, shows that the most southern race is the smallest of the four. *Canaster* and *rileyi* are larger than *alleni* in these measurements but *erythrophthalmus* is smaller than the former two. In this case *erythrophthalmus* may conform to the rule in relation to *canaster* and *rileyi*. *Alleni*, however, apparently does not conform in relation to any of the other forms.

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[1] Miller (1941: 354), in his detailed investigation of variation in *Junco*, concluded that wing and tail length in this genus were largely independent of body size.

Gloger's Rule. "The melanins increase in the warm and humid parts of the range. Reddish or yellowish brown phaeomelanins prevail in arid climates where the blackish eumelanins are reduced. The phaeomelanins are reduced in cold climate, and in extreme cases also the eumelanin (polar white)." In examination of this rule it was felt that the breeding season was the critical period. For this reason July values for this environmental factor were examined (Weather Bureau: 1897). The breeding range of *alleni* has the highest relative humidity. The average for two stations is 83.0. *Rileyi* inhabits the next most humid area, two stations averaging 81.0. The range of *canaster* is slightly less humid, averaging 80.3 for six stations. The more northern and inland range of *erythrophthalmus* is considerably less humid; 12 stations average 70.2. In both the males and females the northern form, inhabiting an area of lowest relative humidity, shows an increase in the reddish pigments present. *Canaster* is grayer than *erythrophthalmus*. *Rileyi* shows more red on the plumage than does *canaster*, but not as much as *erythrophthalmus*. The plumage of *alleni* is not darker than these, but rather more gray, as if due to bleaching. Thus, *rileyi* and *alleni* appear to conform to this rule as a unit. *Canaster* and *erythrophthalmus*, when viewed together, also appear to conform to Gloger's rule. When the whole species is considered, however, a lack of conformity is evident.

Rensch's Clutch Rule. "The races of a species which live in the cooler parts of the range of that species lay more eggs per clutch than the races in the warmer parts of the range." Todd (1940) and Roberts (1932) report for western Pennsylvania and Minnesota, respectively, average egg clutches of four to five. Howell (1932) records the average size of clutch in Florida as three. Sprunt and Chamberlin (1949) indicate clutches of two to five for *canaster* in South Carolina. With the scanty data available general agreement with this rule appears to be the case.

Rensch's Wing Rule. "The wings of races that live in a cold climate or in the high mountains are relatively longer than those of the races that live in the lowlands or in a warm climate." *Alleni* is the only race which shows conformity with this rule. In its relationship to *rileyi*, *canaster* and *erythrophthalmus*, the wing of *alleni* shows considerable shortening. *Erythrophthalmus*, however, has a mean wing length which is not longer than that found in *canaster* and *rileyi*, but shorter.

Mayr's Rule (1942: 92). "Races in the cooler climates are more strongly migratory than the more southerly one." *Pipilo erythrophthalmus* does not conform to this rule as indicated in the discussion of migratory behavior in this report.

Biotic Areas

Dice's (1943) Biotic Provinces have been scrutinized in this connection and little conformity of racial distribution with those provinces is evident except in *erythrophthalmus*. This race is distributed in an approximation of Dice's Canadian, Illinoian and Carolinian provinces. The other three races, however, are mainly contained in his single Austroriparian province.

Conformity of racial distribution of towhees to the Life Zones of Merriam et al. (1910) presents much the same picture. *P. e. erythrophthalmus* breeds in the eastern part of the Upper Austral and Transition zones. The differentiation of *canaster*, *rileyi* and *alleni* within the Lower Austral Zones does not conform with the proposals of either Dice or Merriam with regard to environmental sameness for this area.

Temperature Zones

Visher (1944) presented a series of seventeen maps concerned with freezing temperatures in the United States. His Figure 17, based on the duration and severity of freezing temperatures, divides the United States into six zones. These zones approximate fairly closely those of Merriam, except in the extreme southeast. Visher's data indicate that southern Florida, northern Florida and the Gulf Coast, and the Piedmont and Coastal Plains areas of the southeast should be considered as different from one another in respect to freezing temperatures. Calhoun (1947) concluded that there was correlation of size in *Passer domesticus* with the thermal lines drawn by Visher. Visher's zones 4, 5, and 6 cover the range of *erythrophthalmus*. The southern limit of zone 4 closely approximates the southern limit of this race during the breeding season. Zone 3 contains *canaster* in its western, and *rileyi* in its eastern portion. The southern limit of this zone conforms favorably with the southern limit of these two races. *P. e. alleni* ranges over Visher's zones 1 and 2. There is approximate conformity of racial distribution to these zones.

It appears that the various ecological rule, biotic province, life zone and temperature zone correlations are of most importance in dealing with non-migratory species. Migrating populations for the most part avoid the selective effect of lowered winter temperatures by simply moving away from them. The few stragglers that remain in the far north must be of little importance when considered with respect to the whole population.

Historical Factors

In view of the fact that present environmental factors do not appear to furnish an entirely adequate explanation for the geographic variation within the species, some other factors must be considered. As mentioned earlier great difficulty is experienced in arriving at a conclusion as to whether the (1) southeastern races represent an extension of the range of the northern population (or vice versa) or whether (2) *canaster* and *rileyi* are representative of extensions of formerly isolated populations which are now meeting and intergrading in the middle ground of the southeast.

The possibility of stabilization of genotype as a result of a narrowing front as the continental population pushed south into Florida must be considered. The narrowing would not become pronounced until the species moved down onto the Coastal Plain. It furnishes no explanation for the differentiation of *canaster* and *erythrophthalmus,* whose line of junction is not appreciably narrowed. The junctions between *canaster* and *rileyi,* and *rileyi* and *alleni* are successively narrower. It is possible to visualize, particularly in the case of *alleni,* stabilization taking place as a result of this radical narrowing. *P. e. alleni,* however, is not the most perplexing of the races here considered. In many respects, as already noted, this form shows the effects of environmental selection in agreement with several of the ecological rules surveyed.

In connection with the second proposal, a review of some of the geological events which occurred in the Cenozoic is to the point. Cooke (1945: 3) concludes that the Floridian Plateau has always been a part of the continental mass as distinguished from the deep sea. There appears to be little question that throughout Tertiary time peninsulas or islands of varying shapes and sizes existed in the present area which constitutes Florida. There certainly have been periods during pre-Oligocene epochs when all of this area was under water, but the evidence available seems to indicate the possibility that several island areas may have been above water ever since that time.

White (1942: 29–47, figs. 5–9) discusses the history of this area based on evidences from geology and paleogeography. Much of his information comes from a vertebrate fossil deposit in Gilchrist County, Florida, near Bell. He concludes that following the withdrawal of the Eocene seas, there was a series of crustal movements which resulted in the formation of the Central Florida Dome. At the same time there was a down-warping of the strata across the northern end of the plateau to form the Okefenokee Trough. During the Lower Oligocene the sea invaded the Okefenokee Trough only far enough to form a large bay at either end, with a pedunculate land mass extending southeastward from the mainland of North America.

During Middle Oligocene (Marianna time), with further crustal movements occurring, there was a deepening of the Okefenokee Trough, and the Gulf communicated with the Atlantic across north Florida and south Georgia through straits 50 or 60 miles wide. At the close of this period of submergence there was a general withdrawal of the seas, and Florida was again connected with the mainland.

The late Upper Oligocene saw the reduction of this land mass to a small island, located in what is now the northwestern part of the peninsula, roughly 150 miles from the nearest mainland. The vertebrate fossil material at Bell, Florida, contradicts Schuchert's (1935: 231) earlier concept of the general submergence of the Florida peninsula by the advancing Lower Miocene seas. White (*op. cit.*: 42) states:

> "During the period of time represented by the fluvial deposit in Gilchrist Co. [Lower Miocene], Florida was a limestone island cut off from the mainland by a shallow sea fifty or sixty miles wide. In Tampa time Florida was an elliptical island roughly 220 miles north-south by 100 east-west. . . .
>
> "If the structure of Florida. .... during the Lower Miocene was at all similar to that of today the highest part of the island would have had an elevation of about 200 feet. This is not enough seriously to affect the climate. There is no reason to suppose that the climate was very different then than now."

Throughout the Miocene there was further withdrawal of the seas. It appears that from this time forward there has certainly been some land, in the form of large islands or a group of keys, present in central Florida.

The emerging land mass, indicated as having appeared during the late Miocene, in Pliocene time became a peninsula forecasting the shape of the state today. The area south of the present latitude of Lake Okeechobee was covered by a shallow sea (Campbell, 1940: 104).

During the Pleistocene, peninsular conditions were permanently established, following the several oscillations of sea level attendant to the fluctuation of the ice caps. The Pleistocene history of the extreme southeastern United States has been reviewed by Cooke (1939). He states that there were at least six fluctuations of sea level during this period — from 270 feet above, to 230 or 300 feet below the present level. The highest rise of water, attained at the beginning of the Pleistocene, produced the Brandywine Terrace. At this time all of Florida was submerged, except for a group or groups of islands located in what is now mid-peninsular Florida, at about the latitude of Tampa. A scattered chain of small islands extended northward into middle southeastern Georgia. Much of the present range of *P. e. rileyi* was under water at this time. Following this high level of water, there was a fall to 230 or 300 feet below the present sea level; a rise of 100 feet above and an intermittent fall to 60 feet below; an intermittent rise to 25 feet above and a drop to an undetermined low; and a last rise to the present level. Cooke further states that there has been no crustal movement during this period, as evidenced by the unbroken beach terraces in this area created by the oscillations of sea level.

The present Florida race, *alleni*, may be a relict form. Carr (1940: 6) in his study of the relict herpetofauna of this area places the Florida relicts in two classes: "(1) those derived *in situ*, from living or extinct or subsequently modified ancestral stocks, either by isolation on a Pliocene island or islands (or as I believe less likely, on Pleistocene Islands), or else by ecesic isolation; and (2) those which represent the remnant of a once widespread pre-Pleistocene stock."

That birds inhabited these island and peninsular land masses there is no doubt. Wetmore (1943) has examined avian material from Pierce, Polk County, Florida, and from the Bell locality. The material from Bell has been assigned to Lower Miocene by White and contains "a peculiar shorebird of a hitherto unknown type, a dove, and a wood warbler." The shorebird has been designated by Wetmore as the type of an extinct family. The other two species have not been identified. The Pierce fossils have been attributed to Middle Pliocene deposits by White and consist of *Gavia palaeodytes* Wetmore, *Diomedea anglica* Lydekker and *Phalacrocorax auritus* (Lesson). These forms, all marine or aquatic in habits, do not necessarily indicate the existence of nearby land masses, except as the needs for breeding grounds arose. Of additional interest in connection with the present discussion of variation is Wetmore's comment concerning his assignment of the cormorant material of Pliocene age to the modern species. He says, "unquestionably they appear to belong to this the modern species. . . . "

Certainly the possibility exists that either during Pliocene or post-Pliocene time a segment of a continental population of birds might have become isolated in this area. The barrier causing isolation does not have to be visualized as consisting of simply the straits or narrow necks of land that have existed between Florida and the continent at various times during this period. Even with the connection re-established for varying periods of time, ecesic barriers may have prevented re-uniting of the previously isolated segments.

If these events have occurred then one might expect to find some evidence of their occurrence reflected in the present populations. In the review of the migratory behavior of the four races, it was pointed out that the movements of *rileyi* and *erythrophthalmus* are much more pronounced than those of *canaster* and *alleni*. If *rileyi* is viewed as the northward extension of *alleni*, it may be thought of as returning to its point of origin during the winter. The same may be said of *erythrophthalmus* as it extended from the range of *canaster* northward, following the retreating glaciers of the Pleistocene. The blending of certain characters, such as iris color and tail spot are certainly not in disagreement with such a proposal. The intensification (enlargement) of others such as bill size, wing, tarsus and toe may be due to the hybrid nature of the intermediate populations.

In conformity with Allen's Rule, if *erythrophthalmus* is viewed as the extension of *canaster* northward, it is found that the extremities in this race do show reductions in size. There is no significant difference in wing size in these forms, in contradiction to Rensch's Wing Rule. Mayr's Rule on migration, however, confirms this view, as does Gloger's Rule on color. *Rileyi*, when compared with *alleni*, shows some increase in bill, tarsus and toe, in contradiction of Allen's Rule. The increase in wing length is in agreement with Rensch's Wing Rule, and the migratory behavior of these two races conforms to Mayr's Rule. In the same manner, as pointed out earlier, there is evidence of conformity with Gloger's Rule.

Habitat preference, particularly in the peninsular Florida race, is of interest. *P. e. alleni* shows definite association with the various scrub-type plant communities found near the coasts and in the central lake region. These plant communities are, according to Laessle (1942: 96), representative of the earliest stage of a xerosere, in the area he studied in Putnam County, Florida. Throughout the state they occur on old dune areas where the soil is almost pure white (St. Lucie) or yellow (Lakewood) sand. In this pioneer association, the only tree of any size is the sand pine (*P. clausa*), with a dense undergrowth of dwarfed trees and shrubs. This usually includes several oaks (*Quercus geminata, Q. myrtifolia, Q. Chapmanni*) saw palmetto (*Serenoa repens*), and in some localities rosemary (*Ceratiola ericoides*). From April to September the towhee is found in abundance in such habitats. The oft-mentioned tendency, noted throughout the range of the species, to move into cut-over, second-growth areas may be attributed to the physical similarity of such habitats to those found in pioneer plant associations.

It is reasonable to suppose that such favorable habitats were abundant on the transitory island and peninsular land masses that existed during the latter portions of the Cenozoic. Under such conditions then many opportunities were presented for immigration of a segment of the mainland population.

Several other birds have distributions that lend support to the theory of insular isolation. The Florida Jay, *Aphelocoma coerulescens*, is usually held to be specifically distinct from the far western members of its genus. Geographically far removed from its relatives, this species is best viewed as a relict form. The habitat preference of this species limits its distribution in Florida to typical scrub associations, along the coast and inland. The Florida Grasshopper Sparrow, *Ammodramus savannarum floridanus,* occurs only in the central part of the state. It has allied races in some of the islands of the West Indies, and also has an insular-type distribution in Central America. The discontinuous distribution of the southern races contrasts with the continuous distribution of the forms in the northern United States.

Several other birds, including the Pine-woods and Bachmann's Sparrows (*Aimophila aestivalis aestivalis* and *A. a. bachmanni*), Eastern and Florida Cardinals (*Richmondena cardinalis cardinalis* and *R. c. floridana*) and the Northern and Southern Crested Flycatchers (*Myiarchus crinitus crinitus* and *M. c. boreus*) show lines of junction in west Florida. It is pertinent to note that *P. e. alleni, canaster* and *rileyi* meet in this same area.

In other groups of animals, endemism in the Florida peninsula is well recorded. Hobbs (1942: 12) lists 17 species of freshwater crayfishes (Cambarinae) which he considers as endemic forms. Six of these he believes are relicts. Carr (1940: 6) states that 11 amphibians and reptiles of Florida may be either relict or isolated species. Byers (1930: 289) concludes that the initial Florida Odonata fauna was a Nearctic one, isolated by a sea barrier. According to Berner (1950: 24), there is no necessity to hypothesize that Pleistocene islands existed in Florida so far as the Ephemeroptera are concerned. He adds, however, that there is no evidence to the contrary in the distribution of these forms today.

Professor H. K. Wallace, of the University of Florida, tells me that there is considerable evidence in the wolf spiders (*Geolycosa*) of such insular isolation. Professor H. B. Sherman, of the same institution, has called to my attention the interesting disjunctive distribution of the brown bat, *Eptesicus fuscus,* which has an endemic form in south Florida (Sherman 1936: 107).

The geological history of the peninsula of Florida furnishes abundant evidence of the possibility of isolation occurring during the Pleistocene. Other animals, both vertebrate and invertebrate, apparently were trapped by fluctuating sea levels. Some of these forms, moreover, have never since been able to rejoin the continental stocks from which they were derived, and remain as relict forms within the present peninsula.

Adams (1902) concludes that the southeastern states represent a center of dispersal from which many forms expanded their ranges, after the advance of the Pleistocene ice-caps. Variation in the eastern races of *P. erythrophthalmus* supports this conclusion in many respects.

It is unfortunate that Adams did not consider peninsular Florida in his study of this problem. If his view is correct, and if a segment of this population was isolated on the islands, it appears that the present trends in geographic variation have a rational basis.

I do not feel, on the basis of the evidence at hand, that it is possible to come to any definite conclusion concerning this problem, as it is reflected by this species. It does appear, however, that the greater weight of evidence is on the side of isolation and subsequent merging of populations. Further it seems reasonable to suppose that the pale-eyed Florida stock was derived from living or subsequently modified forms. It does not appear to be the remnant of a once widespread pre-Pleistocene stock.

SUMMARY

A review of the historical status of the species *Pipilo erythrophthalmus* from 1731 to the present is given.

A statistical study of geographical variation in size of body parts and color of irides is presented. A subjective analysis of variation in plumage color is presented. On the basis of these studies recognition of four geographic races within the species is possible. For each of these races there is given:

1. An analytical key to identification.
2. A synopsis of names applied in the past.
3. A description of the characters by which it may be recognized.
4. A discussion of its habits.
5. A statement of the breeding range and migratory behavior.
6. A list of specimens examined.

A detailed analysis of geographical variation in the several characters examined is presented. Non-geographic variation is described. Possible reasons for geographic variation in the species are explored and suggestions are presented in explanation of the patterns observed.

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LITERATURE CITED

Adams, C. C.

1902. Southeastern United States as a center of geographical distribution of flora and fauna. Biol. Bull., **3**(3): 115–131.

Allen, J. A.

1871. On the mammals and winter birds of East Florida, with an examination of certain assumed specific characters in birds, and a sketch of the bird faunae of North America. Bull. Mus. Comp. Zool., **2**: 161–450, 5 pls.

1872. Notes of an ornithological reconnaissance of portions of Kansas, Colorado, Wyoming and Utah. Bull. Mus. Comp. Zool., **3**(6): 113–183.

1878. Addenda to Coues (1878: 41). Notes on spotted birds, at Ft. Leavenworth. Bull. Nutt. Orn. Club, **3**(1): 42.

Amadon, D.

1949. The seventy-five per cent rule for subspecies. Condor, **51**(6): 250–258.

American Ornithologists' Union Committee

1886. The code of nomenclature and check-list of North American birds adopted by the American Ornithologists' Union (New York, Am. Ornith. Union). i–viii + 1–392.

1895. Check-list of North American birds. Second Ed. (New York, Am. Ornith. Union). i–xi + 1–372.

1910. Check-list of North American birds. Third Ed. (New York, Am. Ornith. Union). 1–431, 2 maps.

1916. Changes in the A.O.U. check-list of North American birds proposed since the publication of the sixteenth supplement. Auk, **33**: 425–430.

1923. Eighteenth supplement to the American Ornithologists' Union check-list of North American birds. Auk, **40**: 513–525.

1931. Check-list of North American Birds. Fourth Ed. (Lancaster, Pa., Am. Ornith. Union). i–xix + 1–526.

Baird, S. F., T. M. Brewer, and R. Ridgway

1874. A history of North American birds. Land birds, **2**: i–vi + 1–590 + 6, 30 pls., **3**: i–vi + 1–560 + 28, 8 pls.

Berner, L.

1950. The mayflies of Florida. Univ. Fla. Bio. Sci. Ser. **4**(4): 1–267, 88 figs., 24 pls., 19 maps.

Brodkorb, P.

1935. A sparrow hawk gynandromorph. Auk, **52**: 183–184.

Byers, C. F.

1930. A contribution to the knowledge of Florida Odonata. Univ. Fla. Bio. Sci. Ser., **1**(1): 1–327, 19 figs., 11 pls.

BURLEIGH, T. D.

1937. Bird life on the North Carolina coast. Auk, **54:** 452–460.

1944. The bird life of the Gulf Coast region of Mississippi. Occ. Pap. Mus. Zool. La. State Univ., **20:** 329–490, 1 map, 3 figs.

CALHOUN, J. B.

1947. The role of temperature and natural selection in relation to the variations in the size of the English Sparrow in the United States. Am. Nat., **81:** 203–228, 5 figs.

CAMPBELL, R. B.

1940. Outline of the geological history of peninsular Florida. Proc. Fla. Acad. Sci., **4:** 87–105.

CARR, A. F., JR.

1940. A contribution to the herpetology of Florida. Univ. Fla. Bio. Sci. Ser., **3**(1): 1–118.

CATESBY, M.

1731. The natural history of Carolina, Florida and the Bahama Islands. London: at the expense of the author, Vol. I: i–xii + 1–100, 100 pls.

1754. The natural history of Carolina, Florida and the Bahama Islands. Second Ed. London, Vol. I: 2 + i–viii + 1–120, 120 pls.

1771. Histoire naturelle de la Caroline, de la Florida et des Isles de Bahama. Third Ed. London: Benjamin White, Vol. I: 2 + i–vii + i-xliv, 1–100, 100 pls., 1 map.

CAZIER, M. A., and A. L. BACON

1949. Introduction to quantitative systematics. Bull. Am. Mus. Nat. Hist., **93**(5): 349–388, 12 figs., 11 tabs.

COOKE, C. W.

1939. The scenery of Florida as viewed by a geologist. Bull. Fla. Geol. Surv., **17:** 1–118, 58 figs.

1945. Geology of Florida. Fla. Geol. Surv., Bull. **29:** i–ix + 1–339, 1 map, 47 figs.

COUES, E.

1871. [Untitled footnote.] Am. Nat., **5:** 366.

1878. *Pipilo erythrophthalmus* with spotted scapulars. Bull. Nutt. Orn. Club, **3**(1): 41–42.

DICE, L. R.

1943. The biotic provinces of North America. Ann Arbor, University of Michigan Press, i–vii + 1–73, 1 map.

DWIGHT, J., JR.

1900. The sequence of plumages and moults of the passerine birds of New York. Ann. N. Y. Acad. Sci., **13**(1): 73–360, 7 pls.

GMELIN, J. F.

1788. Caroli A. Linné, Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 13 (Lipsiae, impensis Georg. Emanuel. Baer), **1:** part 2, 501–1032.

HOBBS, H. H.

1942. The crayfishes of Florida. Univ. Fla. Bio. Sci. Ser. **3**(2): 1–179, 24 pls.

HOWELL, A. H.

1913. Descriptions of two new birds from Alabama. Proc. Biol. Soc. Wash., **26:** 202.

1928. Birds of Alabama. 2nd ed. Birmingham: Dept. of Game and Fisheries of Alabama. 1–384, 7 pls., 31 figs.

1932. Florida bird life. Florida Dept. of Game and Fresh Water Fish in cooperation with Bureau of Biological Survey, U.S.D.A. i–xxiv + 1–579, 58 pls., 72 figs.

HUBBS, C. L., and A. PERLMUTTER

1942. Biometric comparison of several samples, with particular refreence to racial investigations. Am. Nat. **76:** 582–589.

KOELZ, W.

1939. Three new subspecies of birds. Proc. Biol. Soc. Wash., **52:** 121–122.

LAESSLE, A. M.

1942. The plant communities of the Welaka Area. Univ. Fla. Bio. Sci. Ser., **4**(1): 1–143, 22 figs., 14 pls.

LINNAEUS, C. (Caroli Linnaei)

1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 10 (Holmiae, impensis direct. Laurentii salvii) **1:** 1–823.

MAERZ, A., and M. R. PAUL

1930. A dictionary of color. New York: McGraw-Hill. i–vi + 1–207, 56 pls.

MAYNARD, C. J.

1878. The birds of Florida, with the water and game birds of eastern North America. C. J. Maynard and Co., Newtonville, Massachusetts. Part **5:** 113–136.

1881. The birds of eastern North America; with original descriptions of all the species which occur east of the Mississippi River, between the Arctic Circle and the Gulf of Mexico, with full notes on their habits, etc. C. J. Maynard and Co., Newtonville, Massachusetts. Rev. ed., i–iv + 1–532, 32 pls.

MAYR, E.

1942. Systematics and the origin of species. New York: Columbia Biological Series, Columbia University Press. i–xiv + 1–334.

MERRIAM, C. H., V. BAILEY, E. W. NELSON, and E. A. PREBLE
1910. Fourth provisional zone map of North America. Washington, D. C.: U. S. Bio. Surv.

MILLER, A. H.
1941. Speciation in the avian genus *Junco*. Univ. Cal. Pub. Zool., **44**: 173–434, 33 figs.
1949. Some concepts of hybridization and intergradation in wild populations of birds. Auk, **66**: 338–342.

MURPHEY, E. E.
1937. Observations on the bird life of the middle Savannah Valley, 1890–1937. Contr. Charleston Mus. **9**, i–vii + 1–61, 1 map.

OBERHOLSER, H. C.
1938. The bird life of Louisiana. State of La. Dept. of Conservation, New Orleans, Bull. **28**, i–xii + 1–834, 45 pls.

PEARSON, T. G., C. S. BRIMLEY, and H. H. BRIMLEY
1942. Birds of North Carolina. Raleigh, N. C.: North Carolina Department of Agriculture, i–xxxii + 1–416, 37 pls., 141 figs.

PHILIPP, P. B.
1910. Annotated list of birds observed (with B. S. Bowdish's bird photographing in the Carolinas). Auk, **27**: 312–322.

RAND, A. L., and M. A. TRAYLOR
1950. The amount of overlap allowable for subspecies. Auk, **67**: 169–183.

RIDGWAY, R.
1901. The birds of North and Middle America. Bull. U. S. N. M. **50**, Pt. I, i–xxx, 1–715, 19 pls.
1912. Color standards and color nomenclature. Washington, D. C., published by the author. i–iii + 1–43, 53 pls.

ROBERTS, T. S.
1932. Birds of Minnesota. Minneapolis: Univ. of Minnesota Press. Vol. II, i–xv + 1–821, 90 pls., 606 figs.

SCHUCHERT, C.
1935. Historical geology of the Antillean-Caribbean region. New York: John Wiley and Sons, Inc., i–xxvi + 1–811, 16 pls., 107 figs.

SHARPE, R. B.
1888. Catalogue of the birds of the British Museum. 12 (Fringillidae). London, British Museum. i–iv + 1–871; 16 col. pls.

SHERMAN, H. B.
1936. A list of the recent land mammals of Florida. Proc. Fla. Acad. Sci., **1**: 102–128.

SIBLEY, C. G.
1950. Species formation in the Red-eyed Towhees of Mexico. Univ. Cal. Pubs. Zool., **50**(2): 109–194, 6 pls., 18 figs.

Simpson, G. G., and A. Roe

1939. Quantitative zoology. New York: McGraw-Hill. i–xvii + 1–414, 52 figs.

1942. A standard frequency distribution method. Am. Mus. Novit. No. **1190**, 1–19, 5 figs., 6 tabs.

Sprunt, A., and E. B. Chamberlin

1949. Birds of South Carolina. Cont. Charleston Mus. **11**, i–xx + 1–585, 34 pls., 48 photos.

Sutton, G. M.

1935. The juvenal plumage and post-juvenal molt in several species of Michigan sparrows. Cranbrook Inst. Sci. Bull., **3**, 1–36, 8 pls.

Todd, W. E. C.

1940. Birds of western Pennsylvania. Pittsburgh: Univ. of Pittsburgh Press. i–xv + 1–710, 23 pls., 1 map.

Vieillot, L. J. P.

1816. Analyse d'une nouvelle ornithologie, elementaire. Paris. 1–70.

1819. Nouveau dictionnaire d'histoire naturelle. Paris. **34** (3): 1–578, 8 pls.

1824. La galerie des oiseaux (etc.). Paris. 300 col. pls., 33 pls.

Visher, S. S.

1944. Freezing temperatures in the United States. Ecology, **25**: 113–117, 17 figs.

Weather Bureau, Report of the Chief

1897. Report of the Chief of the Weather Bureau, U. S. D. A., House Document **42**, No. 166: 1–431, 61 pls.

Wetmore, A.

1937a. Observations on the birds of West Virginia. Proc. U. S. Nat. Mus. **84**: 401–441.

1937b. Notes on the birds of North Carolina. Proc. U. S. Nat. Mus. **90**: 483–530.

1943. Fossil birds from the Tertiary deposits of Florida. Proc. New England Zool. Club, **22**: 59–68, 2 pls.

White, T. E.

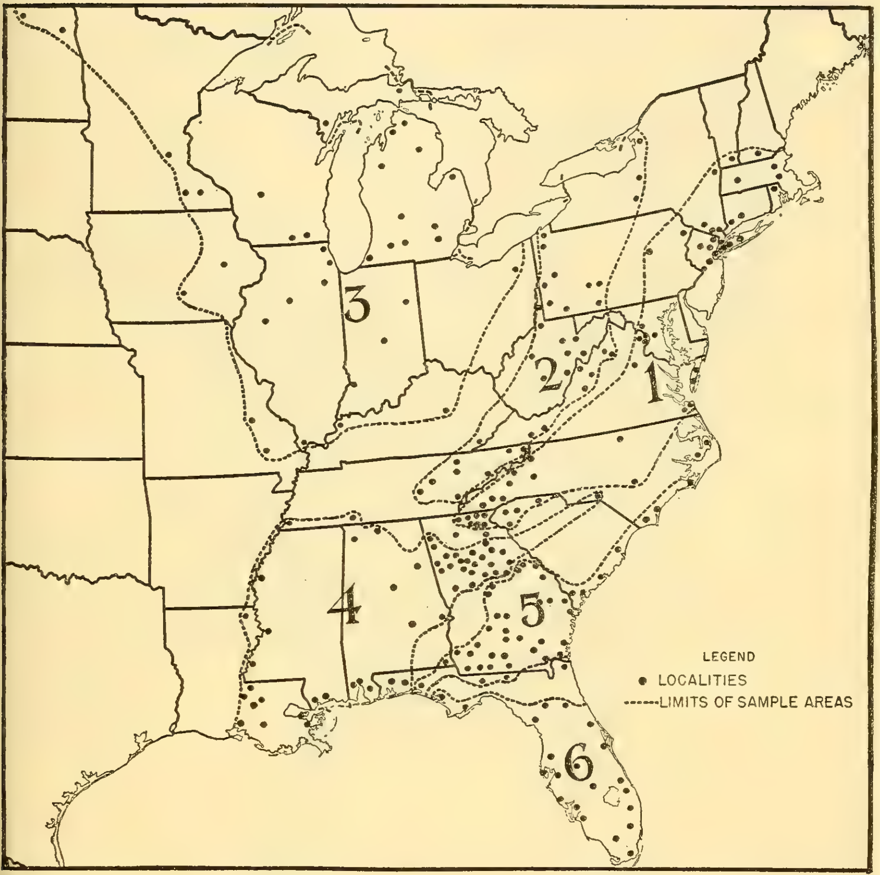
1942. The Lower Miocene mammal fauna of Florida. Bull. Mus. Comp. Zool., **92**(1): 1–49, 14 pls.

Wilson, A., W. Jardine, and C. L. J. Bonaparte

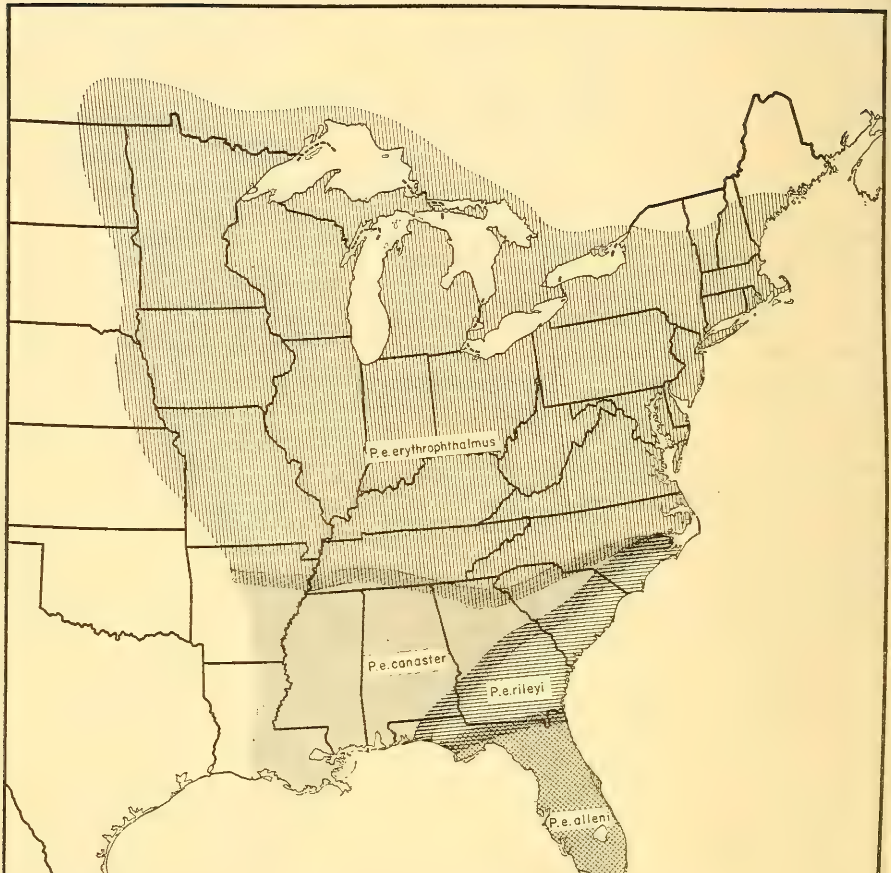
1832. American ornithology. London and Edinburgh. (2) i–vii + 1–390, 33 pls.

Worthington, W. W., and W. E. C. Todd

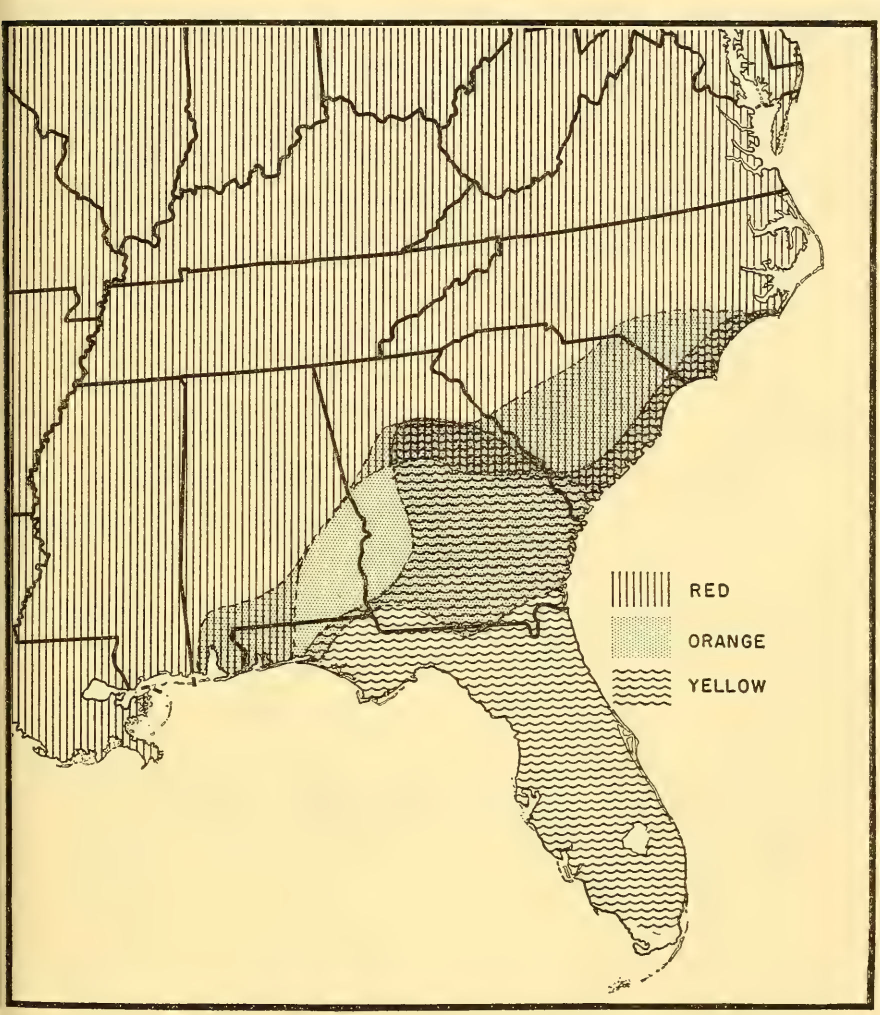
1926. The birds of the Choctawhatchee Bay region of Florida. Wilson Bull., **38** (old series) (4): 204–229.


1
2
3
4
5
6
LEGEND
● LOCALITIES
------LIMITS OF SAMPLE AREAS

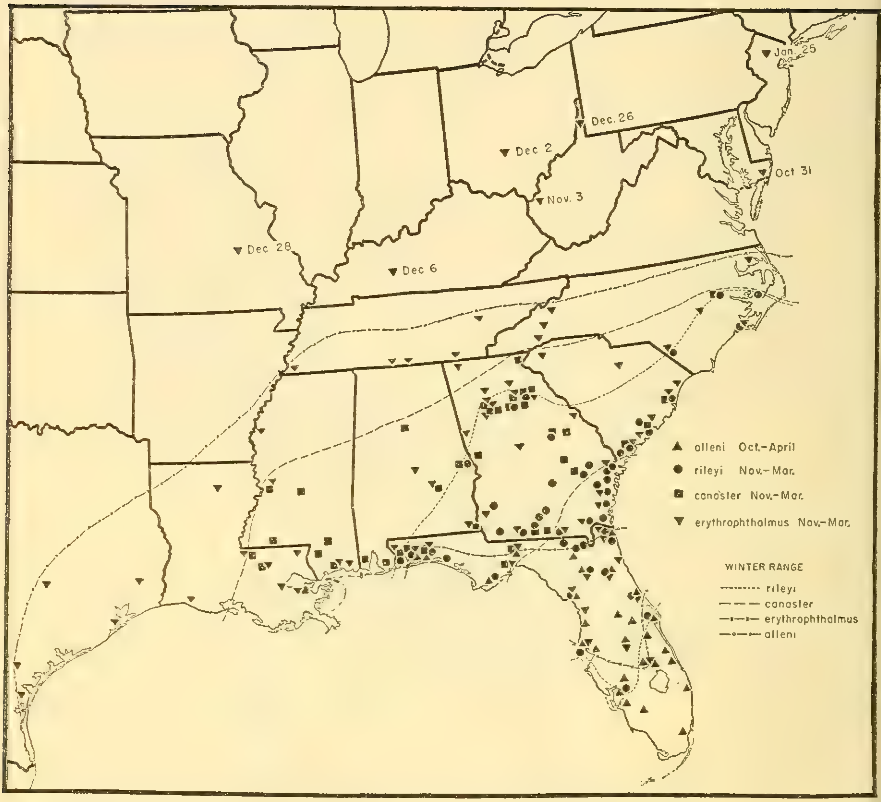
Map 1. Localities and limits of sample areas from which breeding specimens were examined. Samples 1, 2 and 3 represent *P. e. erythrophthalmus*; 4, represents *P. e. canaster*; 5, represents *P. e. rileyi* and 6, represents *P. e. alleni*.


P. e. erythrophthalmus
P. e. canaster
P. e. rileyi
P. e. alleni

Map 2. Breeding ranges of the subspecies of *Pipilo erythrophthalmus*.


RED
ORANGE
YELLOW

Map 3. Geographic variation in iris color in the southeastern United States.


Jan. 25
Dec. 26
Dec 2
Oct 31
Nov. 3
Dec 28
Dec 6
▲ alleni Oct.-April
● rileyi Nov.-Mar.
■ canaster Nov.-Mar.
▼ erythrophthalmus Nov.-Mar.
WINTER RANGE
rileyi
canaster
erythrophthalmus
alleni

Map 4. Winter ranges. Note that *erythrophthalmus* and *rileyi* move farther south in peninsular Florida than does *canaster*.

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By R. H. Flower and R. Wayland-Smith

With Eight Plates

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
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No. 6. — *Cyathaspid Fishes from the Vernon Shale of New York*

By R. H. Flower and R. Wayland-Smith

Cyathaspid fishes are rare elements in Silurian faunas. Only three occurrences have been previously noted in North America, that of *Diplaspis acadica* Matthew from the Upper Silurian of New Brunswick, of *Palaeaspis americana* and *P. bitruncata* described by Claypole (1885) from the Upper Silurian of Pennsylvania, and of *Cyathaspis wardelli* (Ruedemann) and *C. van ingeni* Bryant from the Shawangunk formation of southeastern New York.

The present occurrence, in the Vernon shale in central New York, although it has yielded only eight identifiable specimens, compares very favorably in preservation and completeness of material with previous American finds. It is regrettable that the nature of the exposures makes it extremely improbable that more material can be obtained, particularly since the presence of several species in the association makes the matching of dorsal and ventral plates an extremely inferential matter.

ACKNOWLEDGMENTS

The writers are indebted to Dr. A. S. Romer and Dr. J. C. Bradley for advice concerning problems of nomenclature, and to the following for aid in a search for the original material of Claypole's *Palaeaspis:* Dr. Bobb Schaffer, Dr. David Dunkle, Dr. J. O. Fuller and Dr. W. C. Kraatz.

OCCURRENCE

The Vernon shale, of the Upper Silurian of New York, overlies the Pittsford shale, and underlies the Camillus shales, which are in turn succeeded by the Bertie waterlime. These formations constitute the Salina group, which is overlaid by higher Silurian limestones, the Waterlime group, consisting of the Cobleskill limestone, the Rondout and Manlius limestones. The Vernon shale, characterized by the presence of red and green beds, has yielded a few sparse faunas, but has come to be considered so proverbially barren that the suggestion has been made that it is, at least in a large part, composed of wind blown loess.

Two previous occurrences of fossils have been reported. The first was a recurrent Pittsford fauna, sparsely distributed in shales of the lower part of the Vernon near Pittsford, New York, from which Ruedemann (1920) reported a fauna of sixteen species. Later Eaton (1924) reported a fauna, from which he described several new species, from Elbridge township, fourteen and one-half miles northwest of Syracuse, New York.

The cyathaspid fish described in the following pages came from a layer of grey shale 1 ft. 9 in. thick, in the middle of the Vernon shale. This layer has been found exposed only in two small streams, tributaries of Oneida Creek, about two miles southeast of Kenwood, New York. The complete section, together with the invertebrate faunas, will be described upon another occasion. It will suffice here to mention that this thin layer has yielded several hundred specimens of invertebrate fossils, including abundant pelecypods (*Pterinea*, *Modiolopsis* and *Nuculites*), abundant but extremely fragmentary eurypterids of the genera *Hughmilleria* and *Pterygotus*, ostracods, several poorly preserved nautiloid cephalopods, including one brevicone and several orthoconic genera, brachiopods representing the genera *Lingula* and *Camarotoechia*, an annelid jaw, and a single large siphonophore (Flower and Wayland-Smith, 1947). The invertebrate elements are very closely allied to those of the underlying Pittsford shale and also to those of the younger Bertie waterlime.

The type specimens described in this paper are deposited in the collections of the Museum of Comparative Zoology at Harvard.

CLASSIFICATION OF CYATHASPID FISHES

The history of the study of the Cyathaspida has been summarized by Kiaer and Heintz (1935). In an earlier posthumous paper edited by Heintz, Kiaer (1932) presented a rather elaborate classification of the group. A generation ago, all dorsal plates of these rare and usually fragmentary fossils, were assigned to the genus *Cyathaspis*. After considerable controversy it came to be recognized that a second genus, *Scaphaspis*, was nothing more than the ventral plate of the same animal. It is a far cry from this to the classification of Kiaer, who recognizes the suborder Cyathaspida as divided into two tribes, the Poraspidei and Cyathaspidei, and further divided into seven families and fourteen genera. Unfortunately, problems of recognition and of the legal availability of some of the names used in Kiaer's work, are raised by the fact that some of the species which are new are only listed, while others also new, are listed and illustrated, but not described. This unfortunately applies to the type species of several of the genera erected in this work and to the genus *Eoarchegonaspis* Kiaer and Heintz 1932. Under the present International Rules of Zoological Nomenclature, no species or genus described after 1930 shall be considered valid for the purposes of nomenclature and priority unless it is accompanied by either a description showing how it differs from other species or genera, or by a bibliographic reference to such a description, and in the case of a genus, is accompanied by a clear and unequivocal designation of a genotype.

Later work has resulted in the description of few additional genera and species, mainly those of Bryant and Woodward, but has produced marked and confusing changes in nomenclature. Many of the generic names used by Kiaer (1932) were found to be junior homonyms. New names were proposed by Strand (1934), by Whitley (1940), and by White and Moy-Thomas (1940–1941). Whitley, and White and Moy-Thomas unfortunately proposed new names for the same generic group at about the same time. The names of White and Moy-Thomas are more widely known, but those of Whitley clearly have priority and must therefore be used.

Recent trends in classification have been to employ as families the groups which Kiaer recognized as tribes, and to ignore the finer family divisions as employed by Kiaer. This more conservative treatment is a great improvement, for the much finer family groups which Kiaer used involve both serious problems of nomenclature, as well as serious morphological problems in their recognition. Further, critical analysis of the genera indicates that even the use of two families may imply a more distinct division within the Cyathaspida than actually exists- Moy-Thomas (1939) employed the families Palaeaspidae and Cyathaspidae. The use of *Palaeaspis* as the type of a family, is unfortunate as the genus is inadequately known. Romer (1945) used the families Poraspidae and Cyathaspidae, as employed in the present outline, again treating them as two of the five families of the Heterostraci.

The relationships of the Poraspidae and Cyathaspidae, as noted above, are much closer than a casual reading of Kiaer's paper would lead one to believe and, in fact, serious difficulties attend any attempt to draw a clear line between them. But there is no close connection between the cyathaspids on the one hand, and either the pteraspids or the drepanaspids on the other. It seems that it would be better to either recognize the two families as members of the suborder Cyathaspida, or else to suppress the family Poraspidae, and recognize only a single family, the Cyathaspidae.

In an attempt to determine the generic affinities of our material, it has been necessary to analyse the previous work rather closely. A short account of the results is presented here, partly to clarify the rather intricate nomenclatorial problems, and partly to summarize the present additional morphological information. Particularly relevant to our present problem has been a comparison with the Silurian cyathaspids previously described from America. Of these, the genus *Diplaspis* Matthew proves to be still so poorly known that close comparison is not possible, and its exact position in the modern classification of cyathaspids is extremely dubious. *Palaeaspis* Claypole is still not adequately known, in spite of the work of Bryant (1926). In the same work, Bryant described additional cyathaspids from the Shawangunk formation of southeastern New York as *Cyathaspis wardelli* (Ruedemann) and *C. van ingeni* Bryant. Kiaer has reunited the two species, we think mistakenly, and erected for them the new genus *Eoarchegonaspis*, for which no description is vouchsafed. As shown below, under discussion of the genus, the original suite of specimens of *C. wardelli* consists of inadequate fragments of several cyathaspid plates, representing an indeterminate number of species and certainly including representatives of three different genera. What Bryant described as *C. wardelli* cannot be recognized among Ruedemann's suite of illustrated types. However, in that material there is at least one dorsal shield of *Cyathaspis van ingeni* Bryant. In any case, the genus *Eoarchegonaspis* is a *nomen nudum,* being without a description. None of the fish in the Vernon shale assemblage is conspecific with the Shawangunk materials.

CYATHASPIDA Kiaer

The Cyathaspida are Heterostraci characterized by single dorsal and ventral plates, and a pair of smaller branchial plates. Additional hard parts consist only of large scales which covered the posterior part of the body, and small lateral plates which are rarely found and are poorly known.

Kiaer divided the Cyathaspida into two "tribes", and the tribes into a number of families. This is unfortunate, as tribes are properly a category beneath families and subfamilies in rank. Romer (1945) in his summary of classification of fossil vertebrates, does not employ the families of Kiaer, which are too finely drawn, but instead employs the "tribes" Poraspidei and Cyathaspidei, as families Poraspidae and Cyathaspidae. These families are grouped with others in the Heterostraci without use of the term Cyathaspida to differentiate them from other members of the order. We are employing the term Cyathaspida here because these forms constitute an easily recognizable group, but appalling difficulties were encountered in trying to differentiate between the Poraspidae and Cyathaspidae. Indeed, our own material and the present descriptions and illustrations, lead to the conclusion that these families intergrade to such an extent that their differentiation may have very little merit.

The Poraspidae are defined as having the dorsal plate undivided, and a lateral line system which is well developed, and consists usually of continuous series of canals within the dorsal and ventral plates.

The Cyathaspidae are defined as having the dorsal plate differentiated into a central disc, a rostrum, and two lateral plates, but the lateral line system is incomplete or wanting.

Actually, neither the differentiation of the dorsal plate into distinct areas nor the development of the lateral line system serve to divide the Cyathaspida into two distinct families. Impressions of the interior of the dorsal plate of some poraspids show branchial regions fairly well set off from a central disc. In the genera placed in the Cyathaspidae, the distinction is reported as complete in *Traquairaspis,* as poor in *Tolypelepis,* clear externally in *Cyathaspis,* and variable in *Archegonaspis.* It is apparently clear in the invalid genus *Eoarchegonaspis* Kiaer and *Diplaspis* Matthew. This may be more apparent than real, for these genera are to date represented in the literature only by extremely diagrammatic outline drawings. In the extant illustrations of the Cyathaspida there is no evidence of a clear separation of the dorsal plate into four discrete plates; rather the differentiation is produced mainly by the surface pattern. Indeed, one of our most vexing problems in the description of our new material has been the generic position of a specimen which resembled in some respects *Anglaspis* of the Poraspidae and in others *Archegonaspis* of the Cyathaspidae. So close are these two genera, that the decision was finally made on the basis of the texture of the surface pattern rather than on criteria mentioned in previous descriptions of the families and genera. On the other hand, differentiation of the two anterior lateral plates of the dorsal plate, in *Vernonaspis,* is clear on the interior but not on the exterior. Separation of rostral and lateral areas is not indicated in the suite of syntypes of *Cyathaspis wardelli* Ruedemann, the type species of *Eoarchegonaspis.* It is necessary to conclude that the differentiation of the dorsal plate is not a good basis for the recognition of two families in the Cyathaspida.

The lateral line system is no better as a family criterion. It is a feature difficult to demonstrate, frequently impossible to detect unless there is abundant and well preserved material. It can be seen best in specimens which have been exfoliated, or where the canals are so large that they have been accentuated as depressions on specimens which have been subjected to the slight crushing which accompanies compaction of the sediments. It must be remembered that the Poraspidae from which the lateral lines have been described, are known from the only source of abundant and well preserved cyathaspids, the Spitzbergen material. Genera assigned to the Cyathaspidae, for which in general no lateral lines are reported at all, are known from associations yielding fewer individuals, and apparently, individuals in a much poorer state of preservation. There are certainly grounds for regarding with suspicion the assumption that the lateral line system is wanting in the majority of the genera of the Cyathaspidae simply because it has not been reported. Its value as a family character is therefore doubtful at the best. It is true that in some poraspids — those genera grouped currently under the Poraspidae — the lateral line system forms a complete and sometimes an elaborate series of canals. There are also others in which the canals in the inner layers of the plates form an incomplete and disconnected system of tubes. One such specimen (Pl. 3, fig. 6; Pl. 7; Pl. 8, fig. 3; text fig. 2), consists of a ventral plate. The interior is smooth, but shows a faint pattern of grooves. Upon removing the inner surface by etching (Pl. 7), a disconnected series of tubes of the lateral line system was found. It should be noted that this form, assigned tentatively to *Archegonaspis* of the Cyathaspidae, has the discontinuous canals which are said to characterize that family. However, in *Vernonaspis* (Pl. 1; Pl. 2, fig. 8), there is apparent a series of grooves similar in aspect to a lateral line system. Closer study shows that they are so askew in relation to the symmetry of the organism, that they are more probably wrinkles. Further, if this should prove to be a lateral line system, it would be one comparable with that of the Poraspidae, but this genus, with its distinct rostrum and two anterior lateral plates, is in other respects closer to the Cyathaspidae.

It is necessary to conclude that the boundary between the Poraspidae and Cyathaspidae is, in the present state of our knowledge, too tenuous to be recognized.

The problems of morphology, taxonomic recognition of genera, and their validity from a purely legalistic and nomenclatorial viewpoint, present such intricate problems, that they may be best summarized by a discussion of the individual generic groups. These are arranged, following the system of Kiaer (1932), with the addition of a few subsequently described genera.

PORASPIS

Poraspis Kiaer 1932 (= *Holaspis* Lankester 1873, not Gray 1863) is based upon *Holaspis sericea* Lankester. Dorsal plate entire, surface with essentially longitudinal markings of dentin ridges. Lateral line system represented externally by rows of pores, and well developed. Eye notches clear, branchial and postbranchial regions separated by a faint lateral constriction; posterior margin extended into a blunt median process. Ventral plate truncate in front, similar to dorsal plate in longitudinal markings. Lateral line system less well developed, with two main lateral branches. The genus is best known from the beautiful series of species from Spitzbergen described and admirably illustrated by Kiaer and Heintz (1935). Eleven species are listed by Kiaer (1932) including those later described by Kiaer and Heintz (1935).

Internal molds of the dorsal plate of *Poraspis* are quite similar to those of other genera, but *Poraspis* shows the following distinctive features: the first two pairs of branchial impressions are well anterior to the semicircular canals and prominent, instead of faint; lateral areas are distinct and bear lateral branchial impressions. In general, the semicircular canals are more prominent than the pineal body.

HOMALASPIDELLA

Homalaspidella Strand 1934 (= *Homalaspis* Kiaer 1932, not Reinhardt 1860; = *Homaspis* Kiaer and Heintz 1935, not Foerster 1868 or Skuse 1888) contains only the type species, *H. nitida* (Kiaer). It is differentiated from *Poraspis* by the polished surface and the very narrow grooves separating the dentin ridges. The lateral line system of the venter is more advanced, showing anterior median lateral commissures as well as the marginal lateral commissures.

These two genera are closely allied, but do not seem distinct enough from the following forms, particularly *Anglaspis*, to justify their separation into a family by themselves as was done by Kiaer (1932).

AMERICASPIS

Whitley (1940) proposed the name *Americaspis* to replace *Palaeaspis* Claypole 1885, not Gray. Claypole proposed this generic name for two species from the Upper Silurian of Pennsylvania, *P. americana* and *P. bitruncata*, the former being the genotype. He later stated (1892) that he considered *P. bitruncata* to represent a ventral plate of *P. americana*. His descriptions are accompanied by drawings, giving for *P. americana* the shape of the plate and something of its surface pattern but only the outline of *P. bitruncata*.

Bryant (1926) restudied the species on the basis of material in the Princeton University collections, but without having access to the type specimens. He re-illustrated the species with exceptionally poor photographs, presented revised descriptions, and dismissed with little comment Claypole's suggestion that *P. bitruncata* was the ventral plate of *P. americana.* It is unfortunately quite evident that what Bryant called *P. bitruncata* does not agree at all closely with Claypole's original description or outline drawing of that species, but was almost certainly the dorsal plate of quite another form. Indeed, Claypole's original drawing of *P. bitruncata* quite evidently does have the form of a ventral and not a dorsal plate, and is quite similar in shape to the specimen here described and illustrated as the ventral plate of *Vernonaspis leonardi* (Pl. 2, figs. 6–7).

Unfortunately, an effort to locate the Claypole types proved fruitless. This material was deposited in the collections of Buchtell College, Akron, Ohio, where Dr. Claypole taught from 1884 to 1897. The building which housed these collections was destroyed by fire in 1899, and there is little doubt that the types were destroyed at that time. Dr. Walter C. Kraatz assures me that the material is not in the collections of the University of Akron, which houses the extant records of Buchtell College; the collections were apparently completely destroyed.

Kiaer (1932) treats this genus under the name *Palaeaspis,* and apparently bases his conclusions upon Bryant's redescriptions of the two species. He considers that *P. americana* should be united with his genus *Dinaspis,* and *P. bitruncata* with the genus *Poraspis,* accepting both as dorsal shields. He then calmly proceeds to erect for it the family Palaeaspidae.

Actually, so little is known of the two species which constitute the genus *Americaspis* (= *Palaeaspis* Claypole) that restudy is necessary if the genus is to be considered in relation to the present classification of cyathaspid fishes. In view of the destruction of the type material, careful restudy of the problem is required to determine whether it will be possible to re-establish these species and the genus, on the basis of neotype material. Otherwise it will be necessary to admit that *P. americana* and *P. bitruncata* cannot be recognized with certainty. Therefore the genus *Americaspis* (= *Palaeaspis*) is regarded as valid from the nomenclatorial point of view, but one which is so inadequately known that no species can be referred to it. Even its type species cannot be recognized. Judging from the association of the Vernon shale, and also those in the Shawangunk and Longwood formations of southeastern New York, it will be remarkable if only one genus is present in the association of the Upper Silurian shales of Pennsylvania, which yielded the original material of *Palaeaspis,* as well as all subsequent specimens attributed to the genus and its two species.

DINASPIDELLA Strand

Dinaspidella Strand 1934 was proposed to replace *Dinaspis* Kiaer 1932, not Leonardi 1911. The generic group may be a valid one, and it is therefore discussed here. However, both of the species which Kiaer places in it are *nomina nuda,* since neither has been described. One is only listed; the other, the type species of the genus, is listed and illustrated but not described. In this and in the following genus the ventral plate is five-sided, broadly truncate in front, widest near the posterior margin, which is produced behind into a broad blunt point. In *Dinaspidella* two pairs of longitudinal commissures mark the lateral line system of the dorsal plate.

IRREGULARASPIS Zych

Irregularaspis Zych was described only in Polish, which did not help in its general recognition in the least. White and Moy-Thomas (1940) state that it is the same genus as *Dictyaspis* Kiaer 1932. *Dictyaspis* is another genus which Kiaer described without any valid species. He refers to it three species, again illustrating but not describing the genotype. The genus is characterized by a ventral plate similar in form to that of the preceding genus. On both the dorsal and ventral plates the lateral line system is enlarged into a complex reticular network, quite unlike that of any other cyathaspid.

It should be noted that the family Dinaspidae of Kiaer 1932, erected for *Dinaspis* and *Dictyaspis,* is not legally available since *Dinaspis* rests upon a species which is a *nomen nudum.* In any case, since *Dinaspis* is a junior homonym, a new family name would have to be proposed if there is any point in doing so. While the striking similarity in the shape of the ventral plates suggests a close relationship between these genera, it does not seem that a group embracing them should have family rank.

ANGLASPIS Jaekel

This genus is defined for the first time by Kiaer, who also erects a family, Anglaspidae, for it. This does not seem necessary. *Anglaspis,* based upon *Cyathaspis mcculloughi* Woodward, has been more extensively restudied and re-illustrated by Wills (1935). Kiaer considers as one of the significant features of this genus the fact that the dorsal plate is relatively flat, the ventral plate very strongly arched. The lateral line system is very similar to that of *Poraspis,* with two pairs of longitudinal commissures in the dorsal plate, two series of short transverse pairs of lines on the venter, and a pair of longitudinal commissures at the extreme sides. Dentin ridges are well defined, prominent, in the main, forming a longitudinal pattern. An anterior triangular area is a conspicuous feature, embracing the rostral area and terminating in a point just behind the pineal body. The margins of this area correspond to a part of the lateral commissures of the lateral line system. In a part of this area a faint transverse line differentiates the rostrum on the exterior, and laterally the lateral line system is again responsible for differentiation of two lateral areas from a central disc. In this respect, the genus *Anglaspis* approaches the Cyathaspidae to such an extent that it might as well be considered a member of that family (= tribe Cyathaspidei as used by Kiaer) instead of the Poraspidae (= Poraspidei of Kiaer). The shape of the dorsal shield is somewhat varied, but the eye notches are developed, the sides are more convex than in *Poraspis,* and the branchial and postbranchial regions more poorly differentiated. The posterior margin is pointed at an angle sharp enough that the lateral angles at its sides are obtuse and sometimes obscure. Impressions of the interior of the dorsal plate resemble those of *Poraspis,* but the pineal body is more prominent, the mesocephalon more obscure; the anterior branchial grooves are more obscure, the anterior portion more transverse, and the nasal pits more pronounced. The ventral plate is quite similar to that of *Poraspis*; all species show much finer texture in the surface markings than does *Poraspis.* It should be added that the branchial plates are well known as are the posterior body scales, on the basis of which Kiaer (1932) has reconstructed the entire animal. In addition to the genotype, Kiaer lists four new species and one variety, which have not yet been described.

CTENASPIS Kiaer 1930

This genus is set apart by its striking form and ornament. Anterior part of dorsal shield transverse, sides rounded, widest near posterior margin, which is pointed behind, and joins the convex sides without a definite angle; main part of shield pustulose, sides with definite spines at the margins. Ventral shield more sharply transverse in front, posterior margin somewhat more distinct from sides. Lateral line system well developed, somewhat more advanced than in *Poraspis.* Two species from Spitzbergen, *C. dentata* and *C. cancellata* are all that are known. The former is the genotype. Kiaer (1930) erected a family for the reception of this genus alone.

CYATHASPIS Lankester

The genus *Cyathaspis,* which formerly embraced all cyathaspid fish, is now considered to be confined to the type species, *C. banksi* Huxley and Salter. Dorsal shield a broad oval, longer than wide, narrowly rounded in front, and narrowing also behind; without a clear boundary between the lateral and posterior margins. Main part of plate with dentin ridges forming a concentric pattern, in which a prominent feature is a depression separating the rostral and lateral areas from the central disc; the separation of the rostrum from the lateral plates is more obscure. A low narrow raised ridge occurs on the posterior part of the dorsal shield. The ventral shield, originally described as *Scaphaspis truncatus* Lankester, was the center of some controversy before its identity with *C. banksi* was generally admitted (see Kiaer and Heintz, 1935, pp. 32–33); and as stated by Woodward (1891, p. 172), it is not at all certain that all of the ventral shields placed under this name belong to the same species. Kiaer (1932, pl. 8) has presented beautiful illustrations of dorsal and ventral shields. Differences in the character of the ornament are shown here that remind one of Woodward's statement, but may be due to different conditions of preservation, for the dorsal shield appears to have the internal features impressed on the exterior. Nothing is known of the lateral line system.

ARCHEGONASPIS Jaekel

This genus, proposed by Jaekel (1927) without any very clear diagnosis, is based upon *Cyathaspis integer* (Kunth, 1872). It is better known from Kiaer's (1932) definition. Dorsal plate with rostral and lateral areas well differentiated on the basis of the surface pattern; dentin ridges on rostrum transverse, arranged in two coalesced whorls, one centered near each side. As in *Anglaspis,* the rostrum forms part of a triangular area of the surface pattern which terminates in a point just behind the pineal body. Though nothing is stated concerning this area, its boundaries are in all probability a part of the lateral line system, which is not otherwise evident from extant descriptions or illustrations. Additional pores are present on the dorsal surface, suggesting a more extensive lateral line system. Ventral plate sharply truncate in front, broadest near posterior margin which is convex, apparently not greatly produced, and with only a short production of the center into a point, or else transverse. The posterior margin of the dorsal plate is faintly convex, but nearly transverse, and not pointed. Kiaer (1932) lists four species, all valid, except that he fails to state on what basis he erects a species *A. lindstrømi* for the specimen which Lindstrøm (1895) assigned to *Cyathaspis? schmidti*. This is, however, probably the best known of the species, from the illustrations of Lindstrøm and Kiaer. This species is from the Upper Silurian of Skaane, Sweden. The other four are from erratic blocks in northern Germany.

The interior of the dorsal shield presents no features by which it can be separated with certainty from *Anglaspis*, other than the more transverse condition of the posterior margin. Indeed, the genera are quite similar. Kunth's (1872) illustrations of the type species indicate that, as in *Anglaspis*, the ventral shield is much more strongly arched than the dorsal shield; Kiaer states that the body scales are imperfectly known but also show a similarity with *Anglaspis* as far as can be told. These genera, then, appear to be separated mainly on matters of degree; in *Anglaspis* the ribbing of the surface is coarser; the posterior margin is more produced, the lateral line system is better developed, or perhaps only better observed, and the rostral and lateral areas are less distinctly set off from the central shield. One could wish for clearer differences.

EOARCHEGONASPIS Kiaer 1932

Original description:

"This new genus is established for the two forms known from America and described under the names of *Cyathaspis wardelli* Bryant and *Cyathaspis van ingeni* Bryant.

"The present writer regards these two forms as representatives of the *angusta* and *lata* forms, and therefore proposes to retain only the name *Eoarchegonaspis wardelli* Bryant. After the descriptions of Bryant it must be regarded as being closely related to the *Cyathaspis* and *Archegonaspis*, but it shows some features which make it necessary to establish a new genus for it. All the material of this form is known from the beds of Red shale in the part of the Yerguard Quarzit, Orange County, N. Y. These beds probably belong to the Medina formation."

This genus, happily, need not be recognized under the International Rules of Zoological Nomenclature. Kiaer states that in his opinion the genus is different, but does not say what the features are which impelled him to erect this new genus.

There are several minor errors in this description. The type species is to be attributed not to Bryant, but to Ruedemann, who described it as a species of *Anatifopsis* Barrande, a genus supposedly belonging to the cirripedes.

The material came from a formation proposed by Van Ingen, the Guymard quartzite, of Orange County, New York. Today this formation name is not generally used, and these beds are included in the Shawangunk conglomerate which grades upward into the Longwood shale.

These beds have been considered by many to be of Medina age, Lower Silurian, and therefore older than the other American Silurian cyathaspids. The supposedly greater age may have been at least a strong influencing factor in impelling Kiaer to erect a new genus for this material. The greater age of these beds is not, however, proved. The Medina age determination rests mainly upon the presence in the Shawangunk formation of the trail *Arthrophycus,* which is, to be sure, the abundant and conspicuous feature of the Medina sandstone in western New York, but is hardly an adequate or a reliable criterion for age determination. Overlying the Shawangunk and the almost equally barren Longwood shales, are fossiliferous beds of upper Cayugan age, the equivalent of the Cobleskill limestone, and it is therefore possible for these clastic beds to be as young as the Salina, lower Cayugan. It has been suggested that the Shawangunk may be Clinton rather than Medina in age, but there is no real evidence to oppose the view of Clarke (1907) or Hartnagel (1907) that the entire sequence may be no older than the base of the Salina group. If so, the Shawangunk fish are not materially older than those known from the Upper Silurian of Pennsylvania.

In the hope of clearing up the difficulties surrounding the recognition of *Eoarchegonaspis* and its two species, or two forms according to Kiaer, the original types of *Anatifopsis wardelli* Ruedemann and supplementary material from among which they were selected, were examined. It indicates, in brief, that these forms are cyathaspid fish, but too fragmentary for definite specific recognition. There are obviously several species and even several genera in the suite of type specimens. Further, among Ruedemann's type material there are some dorsal shields which are similar to what Bryant called *Cyathaspis van ingeni,* but not a single specimen which can be identified with what Bryant called *Cyathaspis wardelli.*

The type specimens are described briefly as follows:

1. New York State Museum, no. 9612. A strongly convex plate, sides subparallel, the whole rather strongly curved from one side to the other, surface with rather coarse longitudinal lineation, one end bluntly pointed, the other obviously incomplete. This is probably an incomplete ventral shield, but it might be also a part of a rather large branchial plate. Its generic position cannot be determined in relation to the present rather exacting classification.

2. N. Y. State Museum no. 9613. A small elongate plate, slightly curved and longitudinally striate. One end is drawn to a blunt oblique point; the other is broken. This is certainly a branchial plate.

3. N. Y. State Museum no. 9614. An incomplete plate, rounded at the complete end, and asymmetrical; ridges are mainly longitudinal, but concentric around the rounded border. This is obviously one end of a branchial plate.

4. N. Y. State Museum no. 9615. This is the anterior end of a plate, showing the ridges centering about two anterior lateral areas, the front transverse, truncate, but rather obscure. This is, by its shape and surface markings, a ventral plate similar to those known in *Anglaspis* and *Archegonaspis*. The test is remarkably thick on this specimen in comparison to its size.

5. N. Y. State Museum no. 9616 is the impression of the interior of a ventral plate, truncate in front, strongly produced behind, and suggestive of the (invalid) genus *Dinaspidella* and also to some extent, *Irregularaspis*. Unlike most of the other ventral plates, it is extremely flat.

6. N. Y. State Museum no. 9617 (Pl. 3, fig. 7). is a crushed dorsal plate, preserving the anterior end. The front is bluntly pointed; there are good eye notches. The extreme anterior part of the head has a remarkably thick shield, and shows a smooth surface. There is no clear separation of rostral and lateral plates. Ridges, which appear behind the anterior margin, are extremely fine and faint, and quite closely spaced. This appears to be quite similar to the *Cyathaspis van ingeni* of Bryant (1926).

7. N. Y. State Museum no. 9618. (Pl. 3, fig. 1.) A slender curved plate, with a definite ridge on one side, fractured transversely at several points, with longitudinal markings. This is quite plainly the narrow posterior end of a branchial plate.

8. N. Y. State Museum no. 9619 is a broader triangular plate, comparable in form, but not in surface marking to the unidentified triangular plate figured and described here from the Vernon shale.

9. N. Y. State Museum no. 9620. A plate, strongly curved from one side to the other, incompletely exposed, sides subparallel, very thin, with fine linear markings.

10. N. Y. State Museum no. 9621. A strongly convex plate incompletely exposed, of somewhat oval outline, suggesting the strongly convex ventral shields of *Archegonaspis* and *Anglaspis*. No. 9615 may be a smaller conspecific individual.

11. N. Y. State Museum no. 9622. A small piece of a ventral or dorsal plate, weathered, showing the dentin and cancellous layers

with typical cyathaspid structure. It is too poorly preserved for any attempt at generic or specific determination.

12. N. Y. State Museum no. 9623 is the fragmentary impression of the outer surface of a ventral or dorsal plate, showing in addition to the linear markings faint pustules, smaller than those of *Tolypelepis* and *Traquairaspis,* and not closely comparable to those of *Vernonaspis.*

A good drawerful of material has failed to yield any specimens from the original locality that are materially better, but does serve to indicate more strongly that several genera are present. There are, among such specimens, some with broad flat dentin ridges separated by narrow grooves, suggestive, some of *Poraspis* and *Homalaspidella,* others of *Anglaspis.*

None of this material contains anything at all similar to the form which Bryant called *Cyathaspis wardelli.* One such specimen was found (Pl. 2, fig. 4,), but it is from another collection, from the red Longwood shales which lie above the Shawangunk conglomerate. This is the anterior end of a broadly rounded plate, with very faint obscure eye notches. The surface bears dentin ridges which are irregularly arranged, tending to form small whorls over the anterior portion, and more linear, but still irregular and anastomosing, farther back. The pineal body is indistinct, there is no clear separation of the rostrum from the central disc, but there is some indication of a distinction of the lateral plates on the basis of surface irregularities, but this may be false because the whole surface pattern is so irregular, and quite probably variable from one specimen to another. The surface is folded into small wrinkles, a condition which was plainly not original.

This form poses quite another problem. It is quite similar to what Bryant figured as *Palaeaspis americana* (1926, Pl. 1, fig. 1) as well as to his *Cyathaspis wardelli* (his Pl. 4, fig. 1,) but quite unlike a somewhat narrower specimen with more prominent orbital notches, figured by him on Plate 2, figure 6, as *Cyathaspis wardelli.* Again, it appears similar in shape to the internal impressions of the dorsal plate which Bryant figured as *C. wardelli* on his Plate 2, figure 6, and Plate 3, figure 1.

It is essential that a lectotype be designated for *Archegonaspis wardelli.* If a recognizable dorsal plate is chosen from among the suite of type specimens it will have to be a specimen which is conspecific with *Cyathaspis van ingeni* of Bryant. In any case, at least one new name, and possibly two, will be needed for the *C. wardelli* of Bryant, 1926. A more radical step will at least reduce these name changes by one, and eliminate from all possible revival the undefined genus *Eoarchegonaspis.* This can be done by designating instead of a recognizable plate an unrecognizable fragment as the lectotype of

Anatifopsis wardelli Ruedemann. I therefore designate as the lectoholotype of this species New York State Museum no. 9613, which I have illustrated on Plate 2, figure 5. This will at least leave *C. van ingeni* Bryant as based upon much better type specimens than would be the case otherwise, and will require new names only for the material which Bryant called *Cyathaspis wardelli.* It is extremely dubious whether these forms are distinct generically from what has been called *Palaeaspis,* but as noted in the discussion of that genus, restudy of the original materials is impossible, and *Palaeaspis* and its two species may be completely unrecognizable. Any revision will at least require the re-establishing of the type species on neotype material. I propose no new name, specific or generic, for the form which was the *C. wardelli* of Bryant, being of the opinion that such proposals should rest upon better preserved and a larger suite of materials than are now available.

TOLYPELEPIS Pander

Tolypelepis Pander has priority over *Tolypaspis* Schmidt; the former name was employed first for an isolated scale; *Tolypaspis* was proposed for an essentially complete dorsal shield. Kiaer employs Schmidt's generic name and erects the family Tolypaspidae. Dorsal shield oval in outline, very much as in *Cyathaspis,* posterior margin not adequately known. The separation of the rostral and lateral areas is reminiscent of that of *Archegonaspis.* The dorsal surface is given a distinctive appearance by elongate wart-like tubercles, or scale-like ridges. Kiaer states that these structures are marked by a broad median ridge and finer lateral ridges. Actually, from his photograph, each one of these protuberances is broad enough that its elevated portion consists of a central dentin ridge and two lateral ridges, which usually continue beyond these elevated areas, though the surface is quite irregular in this respect. The protuberances usually bear pores, frequently two or more pores to one protuberance. On this basis, something of the lateral line system can be reconstructed. One pair of commissures passes from the margin of the head in front of the eyes obliquely toward a point behind the pineal body, but does not join. The pattern of the remaining pores is less clear, but from what can be seen, there is a lateral line system here not strikingly different from that of *Poraspis.* The elongate wart-like ridges are quite evidently not all equipped with pores, and are not the direct result of the development of a lateral line system. Rather they are the effect produced by the breaking up of such longitudinal ridges, as are present in *Cyathaspis,* into individual elongate units. The only species known is the genotype, *T. undulata* Pander, from the upper Ludlow of Oesel, and possibly present also in the Ludlow of England.

DIPLASPIS Matthew

This genus is known only from the genotype, *Diplaspis acadica* Matthew, 1886. The description is accompanied by an outline drawing showing three plates in addition to a central disc. Although Matthew presents a rather detailed description, the exceedingly diagrammatic illustrations leave some doubt as to what the characters of this genus really are, particularly in view of the fact that diagrams of related forms have been found to exaggerate the distinctness of rostral and lateral plates. Kiaer (1932, p. 25) makes a new family for this form, on which, we gather, he is no better informed than we are: "It differs from all other previously known forms, and must therefore be regarded as a representative of a new family. As the author could not study the original specimen, he refers to Matthew's original description."

TRAQUAIRASPIS Kiaer

Kiaer based this genus upon *Cyathaspis campbelli* Traquair, a species which had been described but not previously illustrated. Kiaer figures a ventral plate and two scales. Kiaer (1932, pp. 25–26) described the genus as follows: "Middle size *Cyathaspidei* with a complete clefting of the dorsal shield into the different parts (rostral, lateral, and the central disc). The anterior part of the lateral plates probably divided as a separate, small supra-orbital plate.

"The central disc roundish in the posterior part without any median keel or spine. Pineal area indistinctly limited. Traces of the pineal organ cannot be seen. The body scales small, probably in more rows than in *Poraspis*.

"The sculpture of the plates with fine, distinct *Psammosteus*-like ridges, which usually are sharply divided into short portions. On the central disc of the dorsal shield the ribs are more irregularly arranged than on the ventral shield. The latter has a well-marked median keel, and the ribs form an elliptical septum with very fine ribs between the gross ones.

"On the lateral and branchial plates a clear median keel with a strong ridge is developed. On both sides of the latter, fine ridges, regularly longitudinally arranged, are placed.

"This genus is represented only by one specimen, *Traquairaspis cambelli* [sic] Traq. The specimen was found by Professor Cambell [sic] in the Downtonian series in Stonehaven area, Scotland."

In the last paragraphs obviously, the word "specimen" is a misprint for "species." Traquair died shortly after publishing a short descrip_ tion of this species without illustrations. Kiaer (1932) has presented beautiful illustrations of a ventral plate and two scales, but the dorsal plate, which supplies the most crucial generic characters remains unillustrated. The longitudinal ridges on the surface are broken, and suggest the longitudinal ridges of a *Cyathaspis* more clearly than do the ridges in *Tolypelepis*. Pores have not been observed.

CORVASPIS Woodward 1934

The genus *Corvaspis* is based upon a single species, *Corvaspis kingi* Woodward 1934, which is known only from a ventral plate. The plate is strongly concave in front, more deeply so than in any other known cyathaspid. The sides of the ventral shield are extremely tuberculate. Dentin ridges are linear except on the sides where they are broken up into tubercles, but are crossed by an irregular network of fine grooves, which is faintly reminiscent of the condition of the lateral line system portrayed by Kiaer (1932) for *Irregularaspis*, under the name of *Dictyaspis*. However, that these ridges are not the lateral line system, is shown clearly by the fact that they obviously have nothing to do with the pores. A similar tuberculated border is unknown in other cyathaspids, although it is approached, though not closely, in the anterior margin of the ventral plate of *Archegonaspis lindstrømi* Kiaer, which was illustrated by Lindstrøm as *Cyathaspis schmidti*.

The emarginate anterior border of *Archegonaspis drummondi* approaches the form of *Corvaspis*, but does not attain it. This species lacks the complex network of *Corvaspis*. It should be noted that without the dorsal plate, it is manifestly impossible to tell whether *Corvaspis* should be assigned to the family Poraspidae or to the Cyathaspidae.

Two Devonian genera have been assigned to the Cyathaspida, which will only be mentioned. *Cyrtaspidicthys* Whitley (1940) antedates by a month *Eucyrtaspis* White and Moy-Thomas. The name replaces *Cyrtaspis* Bryant 1932, not Fischer 1853. Likewise, *Allocryptaspis* Whitley precedes *Bryantaspis* White and Moy-Thomas, proposed to replace *Cryptaspis* Bryant 1934.

DESCRIPTION OF THE VERNON SHALE CYATHASPIDS

As noted in the introduction, the cyathaspids of the Vernon shale consist of only eight good specimens. Considerable vexation has attended attempts to match dorsal and ventral plates, as well as plates showing the outer and inner surfaces. The species are, as a consequence, based upon dorsal shields showing the external features, and the reference of ventral shields or dorsal interiors has been necessarily somewhat inferential. As a consequence, it has seemed wisest to discuss each of these plates separately, leaving as tentative the specific identification of the ventral shields as well as one beautiful dorsal interior. The material may be summarized as follows:

1. A fine dorsal shield, the holotype of *Vernonaspis allenae.*
2. A much smaller dorsal plate, incomplete, but showing a fine impression of the exterior of the crucial anterior end. This is the holotype of *Vernonaspis leonardi.*
3. A fine large dorsal plate, exposing only the inner surface and the impression of the interior. This is assigned tentatively to *V. leonardi.*
4. An essentially complete internal impression of a ventral shield, together with the impression of the exterior of the posterior portion. On the basis of form and surface this is assigned tentatively to the same species.
5. A fine internal impression of a dorsal plate, described as the holotype of *Archegonaspis drummondi.*
6. An impression of the exterior of a nearly complete ventral shield, clearly an *Archegonaspis,* tentatively assigned to the same species as the above.
7. A small triangular plate, possibly a branchial plate, but of uncertain affinities which is briefly described and illustrated, but not named.
8. A ventral plate exposing the interior, and etched to show the lateral line system. This is described as *Archegonaspis* sp.

VERNONASPIS n. gen.

Genotype: *Vernonaspis allenae* n. sp.

This genus is known only from the dorsal shield, which is slender, the anterior end obscurely pointed, widened behind the eyes, slightly constricted before reaching the branchial region, branchial region gently expanded, sides subparallel in postbranchial region, prominent posterior lateral angles, the posterior margin obtusely pointed in the center, straight on either side; marginal band of posterior margin poorly developed. The surface shows an obscure division of the dorsal shield into a central disc, a rostral plate, and two small anterior lateral plates. The lateral plates proper are not distinguished from the central disc throughout most of their length; it is questionable as to whether the two anterior lateral plates are derived from the anterior end of the lateral plates, or from the rostrum. The surface of the rostrum is complexly whorled, centered about two points in the anterior lateral margin, pustulose in the center, transverse behind. Of the two lateral plates, the anterior one is smooth internally; the posterior one bears coarse polygonal markings. On the exterior the ridges are slightly whorled in front, but become linear behind, blending with the pattern of the lateral plates and central disc. On the central disc the pineal body, itself not prominent or sharply elevated, is the center of radiating curved ridges which finally swing back joining the pattern of longitudinal ridges which occupy the greater part of the dorsal surface. They are modified at irregular intervals by pustules arranged in irregular groups. Some of these pustules bear minute pores, an expression of the lateral line system.

Discussion. This remarkable form is unique in the differentiation of the rostrum, in the two anterior lateral plates of small size, and the absence of any clear differentiation of the lateral plates from the central disc. In this respect, the genus is somewhat comparable to the extremely inadequately known genus *Diplaspis*, judging from the outline drawing of the one and only known specimen. Our form is very different in shape, and indeed, *Diplaspis acadica* is so inadequately known that close comparison is not possible. The pustules of the surface suggest a comparison with *Tolypelepis* and *Traquairaspis*, but the nodes of the surface are quite different in appearance in those genera. In *Tolypelepis* the nodes are larger and more wart-like; in *Traquairaspis* they are obviously isolated elements of broken up coarse longitudinal ridges such as are seen in a perfect state in the genus *Cyathaspis*. *Traquairaspis* according to the description of the genus, is said to have the rostral and lateral plates completely separated, and the anterior end of the lateral plate is possibly separated as a distinct plate. In this respect, *Traquairaspis* is closer to *Vernonaspis* than to any other described genus, but in *Vernonaspis* there is not one anterior lateral plate, but two, and the main parts of the lateral plates are not set off from the main part of the central disc.

Strangely, the form most similar superficially to *V. allenae* is not a cyathaspid, but a pteraspid, the form described as *Pteraspis lerichi* Zych (see Pauca, 1941, Pl. 2, fig. 2,) and *P. lerichi* var. *plana* Brontzen (see Pauca, 1941, Pl. 2, fig. 3.) This form is distinct in a number of features, having apparently distinct pineal and ocular plates and a posterior groove for the reception of a dorsal spine on the posterior part of the shield. Fine surface details are not well enough shown to permit a close comparison, but there is no indication of a pattern of linear ridges and pustules. *P. lerichi* is apparently a pteraspid and its resemblance to this cyathaspid is superficial, but it is not at all similar in aspect to *Pteraspis, sensu stricto,* as illustrated by White (1935).

VERNONASPIS ALLENAE n. sp.

Plate 1; Plate 2, figures 3, 8.

This species is known from a single dorsal plate, 31 mm. long, ocular width 11 mm., branchial width 16 mm., with the sides subparallel in the postbranchial region, no definite postbranchial expansion, 13 mm. wide at the posterior lateral angles. Pineal index 7.5 mm., rostrum 5 mm. long, rather bluntly pointed in front, the anterior part with the dentin ridges arranged in whorls about two anterior lateral centers, the central part pustulose, ridges broken and rather irregular, faintly radial in arrangement, transverse along posterior border. In the type, a slightly oblique break behind the rostrum is more conspicuous than the posterior boundary of the rostrum itself, but is clearly adventitous.

On the sides of the rostrum are two small anterior lateral plates, which are roughly rounded. The inner surface of the more anterior of these plates is smooth; the posterior one shows a surface of small polygonal facets, not closely similar to the usual pattern formed by the cancellous layer, but of a considerably coarser pattern. The external impression of this part of the type was available, and a portion of the test of this lateral region was broken away, and a rubber impression was then taken (Pl. 2, fig. 3,) which shows in part the surface pattern over these regions. Though whorled in front, the surface over the greater part of the area occupied by these two plates consists of longitudinal ridges which are very similar to the arrangement of the ridges over the lateral plates and the central disc. The lateral plates are not at all differentiated from the central disc on the basis of the surface features, and their margins are indicated only by broad shallow poorly defined grooves. The greater part of the central disc bears fine longitudinal ridges, modified at intervals by irregular groups of raised rounded pustules. In some of these pustules minute pores are seen, which evidently connect with the lateral line system. The pineal body is in itself poorly defined on the exterior and is not well elevated; in comparison to our other forms it is extremely small and inconspicuous. It is, however, a center from which the ridges of the surface radiate. Those ridges which extend obliquely forward or directly laterad are curved, eventually turning toward the posterior margin, and joining the general pattern of longitudinal ridges. There is no arrangement in the anterior-lateral portion of these ridges into whorls, as in *Vernonaspis leonardi*, and neither is there a strong V-shaped marking, pointing forward and terminating at the pineal body, as in *Anglaspis* and *Archegonaspis*, which, when present, represents a portion of the lateral line system.

The surface of the type shows several faint linear depressions, best shown in Plate 2, figure 8, which simulate the lateral line system, particularly in showing two prominent longitudinal grooves. These grooves are probably adventitious, as they are not centered at all. Indeed the one on the left passes forward from near the median posterior angle directly to the pineal body, which is a behavior shown by no normal part of the lateral line system in other cyathaspids where, instead, neither of the main commissures intersect the pineal body, but pass forward on either side of it.

There is indication of the thin posterior margin, which retains the dentin layer without the cancellous layer beneath, but it is not as well defined in this species as in our other forms.

Discussion. This specimen is remarkable for the very thin condition of the dorsal plate, which was evidently poorly calcified and quite flexible, for it has been flattened somewhat, but bent in the process without developing any of the cracks which are shown by other of our specimens. Although the test was broken in several places, it proved extremely thin, and no definite trace of the usual layers could be found. The cancellous layer was evidently very thin in comparison to that of *Vernonaspis* cf. *leonardi.* However, a similar condition was found in the small holotype of *V. leonardi,* where no cancellous layer could be detected, indicating that this layer was probably not well developed in small and probably immature individuals.

V. allenae is distinguished from *V. leonardi* by the quite different shape, particularly of the anterior end, the constriction of the lateral margins in front of the branchial region and behind the two anterior lateral plates, and by the much larger pustules of the surface. From other species, none of which it resembles closely, it can be distinguished by the characters of the genus.

VERNONASPIS LEONARDI n. sp.

Plate 2, figures 6–7; Plate 3, figure 5; Plate 5, figure 2.

This species is represented by a small incomplete dorsal plate. There is an impression of the interior to which fragments of the plate adhere, the anterior end incomplete, the posterior end missing. The outline is gently rounded at the sides. The anterior end is shown clearly by an external impression, from which a rubber cast was made, which serves as the basis of our illustration (Pl. 3, fig. 5). This shows the anterior end to be slightly truncated, the sides very faintly notched for the reception of the eyes. The pineal body is large and strongly elevated. The rostrum is distinctly set off from the central disc, though the division between the central disc and the lateral plates is again obscure. At the anterior end, prominent depressions separate the anterior end of the lateral plate from the remainder, though both parts bear essentially linear ridges. In front of this, and seemingly attached to the rostrum, is a similar small plate the surface of which shows the ridges developed into whorls, suggestive of the lateral plate figured by Kiaer and Heintz (1935, Pl. 33, fig. 1,) for *Homalaspidella nitida*, but with finer ornamentation.

The pustules of the ridges on the middle part of the plate are tiny, but well elevated. The markings on the posterior part are somewhat irregular, but essentially linear.

A ventral plate tentatively assigned to the same species, on the basis of form, is represented by an internal impression (Pl. 2, figs. 6–7) and an impression of the exterior from which a rubber mold was taken (Pl. 5, fig. 2.)

The internal impression, 26 mm. long, 16 mm. wide, is quite strongly convex and, in flattening, the margin on the right has been bent under the remainder of the specimen. The anterior end which is imperfect, appears to be strongly truncate in front, and scarcely emarginate if at all. The posterior outline is obtusely angled in the middle, the oblique sides straight and meeting the lateral margins at a prominent angle. Lateral margins curved, greatest width attained shortly behind the middle of the plate. The impression of the interior is relatively smooth but (Pl. 2, fig. 7,) shows a series of very faint ridges, which, however, it has proved impossible to distinguish with certainty from the cracks which are the result of slight crushing of the plate in flattening. In part, at least, these represent a portion of the lateral line system as in *Archegonaspis* sp., but no clear pattern can be made out (Fig. 1).

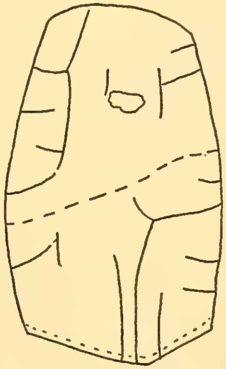


Fig. 1. Ventral shield attributed to *Vernonaspis leonardi*, showing observable pattern of fine ridges, and cracks of the surface, which cannot be properly differentiated. Part of this doubtless represents the lateral line system, which is here very imperfectly preserved.

The surface of the interior in natural color, shows the reticular pattern of the cancellous layer of the shell (Pl. 2, fig. 6.) A small piece of the plate, adhering just orad of the center, fails to show any of the surface features or structure.

The impression of the exterior of the same plate shows only the posterior portion (Pl. 5, fig. 2). The ridges are fine, closely spaced, linear, with irregularly scattered pustules, very tiny in relation to those of *V. allenae*, but suggesting affinities with that form, and comparable to the much smaller pustules of the dorsal plate which is the holotype of *Vernonaspis leonardi*. The internal mold shows a distinct and rather prominent posterior margin to the ventral plate, where, as usual, the cancellous layer is absent and only the dentin layer present.

This ventral plate bears a striking resemblance in outline to Claypole's original drawing of *Palaeaspis bitruncata*, and indicates that this is a true ventral plate as stated by Claypole (1892) and not a distinct species as stated by Bryant (1926). Strict comparison is impossible. Claypole's types have been destroyed, and the original illustration is only an outline drawing. *Palaeaspis bitruncata* cannot, under these circumstances, be recognized with certainty. The reference of this plate to *V. leonardi* rests upon similarity of form and the similarity of the tiny pustules to those of the dorsal plate and holotype.

Cf. *Vernonaspis leonardi*

Plate 3, figures 2–4; Plate 4; Plate 5, figure 1.

Ironically, the largest and finest dorsal plate in the entire collection of Vernon cyathaspids is known from an impression of the interior, and the plate itself, the dorsal surface of which is embedded in the matrix. Under these circumstances, nothing can be ascertained concerning the dorsal surface pattern, which supplies the generic criteria under our present rather finely divided classification. As a consequence, the generic and specific affinities of this form must remain uncertain. The plate has a maximum length of 32 mm., pineal index 6 mm., ocular width 10 mm., branchial width 18 mm., reduced to 17 mm. at the posterior lateral angles. The posterior margin is very thin, there being a well defined marginal band, and the shape of the posterior margin itself is somewhat obscure. There is clearly a blunt median point, as in *V. allenae*, the sides straight or very nearly so on either side of it. The lateral margins of the plate are slightly convex, with no clear differentiation of branchial and postbranchial regions, the anterior end rounded, the ocular impressions faint and very obscure.

There is no clear differentiation between the marginal branchial region and the remainder of the plate, which in most cyathaspids is well marked by shallow grooves on the interior of thed orsal plate, even when no clear separation exists on the basis of the exterior alone.

The impression of the interior shows no clear indications of the nasal sacs. The pineal body is clearly defined and well elevated, behind which is the mesencephalon, represented by two faint vertical ridges, essentially in contact with the semicircular canals, and not distinct from them as in *Archegonaspis drummondi*. The tips of the anterior branches of the semicircular canals are bifid. The medullary ridge is long and well defined in contrast to *A. drummondi*, slightly depressed in the center of the most elevated portion. The branchail impressions are faint, poorly outlined, but the seven pairs can be distinguished. No marginal branchial impressions can be seen.

The interior of the dorsal plate (Pl. 4) shows with remarkable clarity the structure of the cancellous layer, in color. The broken edge, shown in further enlargement in Plate 5, figure 1, shows the usual cyathaspid structure, the thickest and most conspicuous element being the cancellous layer. The surface markings are indicated only in a few small areas where the plate has broken away from the shale, showing a small part of the impression of the exterior. The linear markings in the portion shown are not diagnostic, and agree closely with those of *A. drummondi* as known from the ventral plate, and also *V. leonardi*. The interior of the dorsal plate shows no traces of either a lateral line system, or the differentiation of anterior lateral plates. Slight flattening has caused the plate to be intersected by a series of cracks, widening toward the margin (Pl. 3, figs. 2–3). These have no significance, and fail to parallel any course of a probable lateral line system.

Discussion. The taxonomic position of this dorsal plate is uncertain without the dorsal surface. The transverse condition of the posterior margin is unlike that of most of the "Poraspidei," and is more closely approximated in *Archegonaspis* and in *Vernonaspis* than in any other of the known genera. The character of the interior of the dorsal shield is quite different in several particulars from that of *Archegonaspis drummondi*, particularly in the obscure distinction of the lateral areas, the lack of lateral expansion over the branchial area, and the straight lines which make up the posterior margin of the shield; in *Archegonaspis* these lines are sinuate. A striking feature of this specimen is the thickness of the cancellous layer. Either this is thickened through old age, which is possible, for none of our other specimens approximates this one in size, or else our form is strikingly distinct from any of the other dorsal plates in the present collection.

In shape, this plate agrees strongly with the much smaller holotype of *Vernonaspis leonardi*, and it is tentatively assigned to that species mainly because of this strong resemblance. Two features oppose this determination. The first is the thickness of the cancellous layer which, as noted above, need not necessarily be a determining factor. The second is the absence of any discernible anterior lateral plates. Again, if old age has produced a thickening of the cancellous layer, it may well be accompanied by a secondary fusion of these plates.

As has been noted, the present species shows significant differences in proportions with the previously described genera. None of the Poraspidae is closely similar, and of the Cyathaspidae the only genus known to contain species at all similar in proportions is *Archegonaspis*, and the resemblance even here is not close. The original material of *Palaeaspis americana* was considerably different in outline, the greatest width of the plate being farther forward, and the sides approaching each other behind the middle. However, as pointed out, it is dubious whether this species or genus can be recognized in view of the loss of the type material.

ARCHEGONASPIS DRUMMONDI n. sp.

Plate 2, figures 1–2;

This species is based upon a beautifully preserved specimen, showing only the impression of the interior of a dorsal shield. This shield, 22 mm. in length, pineal index 5.5 mm., has an ocular width of 8 mm., increasing to a branchial width of 13.5 mm. There is no widening toward the posterior end to a definite postbranchial area. The branchial regions are depressed at the edges, and the elevated portion of the plate between them has margins which are essentially straight from the ocular region, diverging gently to the posterior lateral angles, which are 12 mm. across. The angles are rounded, in contrast to their sharp condition in *Vernonaspis*, the posterior margin sinuate, broadly convex in the center instead of coming to a blunt point. A clear narrow posterior border 1 mm. wide is sharply defined; the internal mold shows that here, as in other species, there is only the dentin layer, the cancellous layer being absent, as shown by faint longitudinal striations on the internal mold.

Pineal body large, round, well elevated; nasal sacs at anterior end relatively obscure, not prominently elevated on internal mold as in *Anglaspis*. Three short linear ridges behind the pineal body represent the mesencephalon; they lie between the anterior branches of the semicircular canals which are well elevated and clearly defined. The seven pairs of branchial impressions are broad, shallow, and about of equal clarity from the first to the last. Marginal branchial impressions are not at all evident. The surface over the lateral areas is faintly pustulose, due in part to the presence of fragments of the plate, which as in our other material, was evidently more strongly calcified near the lateral margins. The medullary ridge is forked in front, and lies some distance behind the semicircular canals, between the posterior pair of branchial impressions. It is short, not penetrating into the postbranchial region.

Discussion. Reference of this form to any genus is somewhat hazardous, since the essential generic characters are drawn largely from the features of the exterior rather than the interior of the dorsal plate. However, the extant illustrations are adequate to show that our form is not closely comparable with any of the previously described genera except *Archegonaspis. Poraspis* differs in the somewhat more produced condition of the anterior end, the greater prominence of the nasal sacs, the more anterior position of the pineal body in relation to the branchial impressions, the lateral expansion of a postbranchial area, the obscurity of the posterior margin, and the presence of well defined marginal branchial impressions. The known forms of *Homalaspidella,* though more like the present species in the prominent posterior margin (Kiaer and Heintz, 1935, Pl. 30, fig. 2; see also text fig. 56), resemble *Poraspis* more closely in other features. Much closer to our form in proportions are the interiors of *Anglaspis* and *Archegonaspis,* both in general shape and the arrangement of the impressions of the branchial apparatus and brain. *Archegonaspis* is favored for several reasons. In *Anglaspis* the front of the head tends to be somewhat produced, and the nasal sacs are more prominent, the orbital notches more pronounced, and the posterior margin more strongly produced. Also, a ventral plate, tentatively assigned to this species on the basis of proportions, shows the relatively fine closely spaced striae of *Archegonaspis* instead of the much coarser and deeper markings of an *Anglaspis.* Our material does not show what is considered the crucial difference between the genera, namely whether the dorsal shield is entire as in *Anglapis,* or whether there is a separation of rostral and lateral plates on the basis of the surface marking, as in *Archegonaspis.* As noted in the discussion of these genera, this difference is relatively slight, and actually it is here that there is the closest link between the families Poraspidae and Cyathaspidae.

Archegonaspis cf. *drummondi*

Plate 6

This ventral plate is known only from an impression of the exterior. Our present illustration is taken from an artificial rubber cast. The plate is narrow in front, broadest in the posterior third, the posterior margin bluntly pointed in the middle, the outline essentially straight on either side, and meeting the lateral margin at a well defined angle. The anterior end, obscure, was evidently considerably emarginate. Dentin ridges are longitudinal over the greater part of the length of the shield, but are centered about two whorls on the anterior lateral portions. The ridges are fine, closely spaced. No structures are seen which can be interpreted with certainty as pores of the lateral line system. The plate has a length of 21 mm., a width which increases from 6 mm. at the anterior end to a maximum of 11 mm.

Discussion. This plate in form and surface pattern is typical of *Archegonaspis.* Reference on the basis of such scant material of course uncertain, but the general proportions suggest that this imay have well been the ventral plate of *Archegonaspis drummondi.* It is markedly different in proportions from *Archegonaspis* sp., described below, and differs considerably in texture as well as in outline from the more parallel-sided plate which is tentatively assigned to *Vernonaspis leonardi.*

ARCHEGONASPIS ? sp.

Plate 3, figure 6; Plate 7; Plate 8, figure 3; text figure 2.

Differing from all other forms in its considerable breadth, is a beautifully preserved ventral plate, remarkable for the sharp and slightly eccentric emargination of the anterior end, and the clarity with which the elements of the lateral line system are preserved. This form, we have been unable to identify with any of the other species described above, which is particularly unfortunate in view of the evidence it supplies as to the structure of the lateral line system. The reference to *Archegonaspis* is necessarily tentative, and is based upon the resemblance of its surface pattern to that of *A. drummondi* and also to *A. lindstrømi.* The plate is 24 mm. long, with a maximum width of 14 mm., with the dorsal surface embedded in matrix. The inner surface was essentially smooth, showing cracks due to flattening and a series of faint linear impressions. These are better seen on the impression of the inner surface (Pl. 8, fig. 3, Text fig. 2), than on the inner surface itself. The plate was subjected to gentle etching, which exposed the cancellous layer, the canals of the lateral line system and, in places, the surface pattern of the dentin layer of the exterior, as shown on Plate 7.

In shape, this plate is considerably broader in proportion to its length than other ventral plates encountered in the Vernon shale, showing a strong emargination of the anterior end, best shown in the specimen in its natural color (Pl. 3, fig. 6,) and which is clearly strongly askew. The ventral shield was originally quite strongly curved. Flattening has tended to bend one side more than the other, but is apparently not entirely adequate in itself to account for the eccentric position of the anterior notch. The posterior border meets the lateral edges at sharp and definite angles; it is bluntly pointed in the middle, straight on either side. The posterior thin border of the plate is not as sharply set off from the remainder of the plate as in our other ventral shields, but, as in the other specimens, apparently represents an area in which the cancellous layer is lacking. The surface bears longitudinal dentin ridges as in most species of *Archegonaspis*. These ridges are fine, closely spaced, and probably appear shallower on the exterior than they do from the etched interior shown on Plate 7, for they are not nearly as sharply defined on the impression of the exterior which is shown in the lower left part of the plate as oriented in our figure.

Etching has revealed in addition to the normal features of the dentin and cancellous layers, a series of rather irregularly spaced short transverse canals which represent the lateral line system. Though more irregular and less complete, as series, than those shown for *Poraspis* (Kiaer and Heintz, 1935, fig. 3b, p. 45,) they are clearly analogous to the median portions of the ventral transverse commissures, and the lateral portions of the ventral transverse commissures, though only a very few individual canals of this last series can be detected, and it is not easy to distinguish them from the cracks in the ventral plate which are the result of slight flattening.

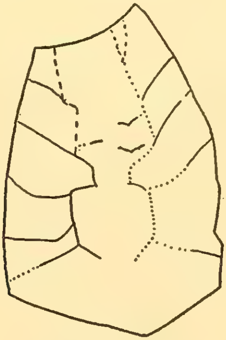


Fig. 2. Outline of *Archegonaspis*? sp., showing reconstruction of canal system from the grooves of the inner surface. Visible portions are indicated in solid lines; indistinct portions by broken lines, frankly inferred connections by dotted lines, where no trace of the canal system could be seen.

Though the matter does not seem to have been discussed in print, it stands to reason that the lateral line system, as a series of neural and sensory organs, must have had a direct connection with the brain and the central nervous system. If so, the incomplete series of canals which are embedded in the ventral plate must have been connected by nerve cords which lay within it, in the tissue of the animal. On the impression of the interior, such a system of canals is suggested by a series of faint ridges, representing, of course, grooves of the inner surface of the plate. They are obscure, low, poorly defined, and somewhat less prominent than the cracks of the ventral plate, in which we are not interested. Their appearance is shown in Plate 8, figure 3. Under favorable lighting, aided by turning the specimen, they can be reconstructed into a much more complete series, illustrated in text figure 2. This shows at least a reasonable series of canals which align with the portions which are embedded in the ventral plate. One possible objection to this explanation is that, prior to etching, no openings were found on the inner surface of the plate which would indicate a connection between the internal canal system, and that embedded in the ventral plate itself.

Discussion. This plate, the only one of our specimens showing clear evidence of the lateral line system, does not seem to match any of the species known from dorsal plates. This is particularly unfortunate because the lateral line system is so imperfectly known in the Cyathaspidae, to which apparently all of our forms belong. It is, however, evident that this form indicates that the differences in the lateral line systems of the Poraspidae and Cyathaspidae are not as marked as has been supposed, Indeed, it must be remembered that the Poraspidae, in which the lateral line system is fairly well known, have been studied on the basis of abundant and well preserved materials, which has not been true of any of the genera assigned to the Cyathaspidae. This fact, together with our present specimen, suggest that the differences are perhaps much more apparent than real and will decrease when more of the Cyathaspidae have been studied from better and more abundant materials.

Unidentified plate

Plate 8, figures 1–2.

This plate is roughly quadrangular, with one angle obtuse and rounded, or may be considered triangular, with one side convex and strongly curved in the middle. The upper side, as oriented in our figure, is perfectly straight; the under side strongly curved, the posterior side straight, forming an acute angle with the upper edge.

Most of the plate has been exfoliated, showing traces of the reticular structure of cancellous layer. Small portions indicate that the surface bore linear markings parallel to the long axis of the plate. As such, the most logical interpretation would be that of a branchial plate, but this form does not agree at all closely with any known branchial plate figured for cyathaspids, the best known being those of *Poraspis* (Kiaer and Heintz, 1935) and *Anglaspis* (Wills, 1935). The form is too blunt and too obtusely pointed to suggest any known spine or scale. Short of a specimen showing a plate similar to this in relation to dorsal and ventral plates, an extremely remote contingency, it will not be possible to refer the present specimen to any genus or species with certainty. Therefore all that is possible is to call attention to this plate and to illustrate it.

BIBLIOGRAPHY

Bryant, W. L.

1926. On the structure of *Palaeaspis* and on the occurrence in the United States of fossil fish belonging to the family Pteraspidae. Proc. Amer. Phil. Soc., **65**: 256 - 271, pls. 1 - 4, 3 figs.

Clarke, J. M.

1907. The Eurypterus shales of the Shawangunk mountains in eastern New York. Bull. New York State Mus., **107**: 295–326, pls. 1–8, 2 figs.

Claypole, E. W.

1885. On the recent discovery of pteraspidian fish in the upper Silurian rocks of North America. Quart. Jour. Geol. Soc. London, **41**: 48–64, 8 figs.

1892. On the structure of the American pteraspidian *Palaeaspis* Claypole, with remarks on the family. Quart. Jour. Geol. Soc. London, **48**: 542–561, 8 figs.

Eaton, H. E.

1924. A Vernon shale (Silurian) fauna in central New York. Bull. New York State Mus., **253**: 111–116, 1 pl.

Flower. R. H. and R. Wayland-Smith

1947. New fauna from the Vernon shale of New York. Bull. Geol. Soc. Amer., **58**: 1180 (abstract).

Hartnagel, C. A.

1907. Upper Siluric and Lower Devonic formations of the Skunnemunk mountain region. Bull. New York State Mus, **107**: 39–54.

Heintz, A.

1933. Neuer Fund von *Archegonaspis* in einem obersilurischen Geschiebe. Zeitschr. f. Geschiebeforschung, Berlin, **9**: 123–131, 5 figs.

1938. Über die ältesten bekannten Wirbeltiere. Die Naturwissenschaften, **26**, heft 4: 49–58, 4 figs.

Jaekel, O.

1927. Die Atemorgane der Wirbeltiere in phylogenetischer Beleuchtung. Zool Anz., **70**: 273–303.

Kiaer, J.

1930. *Ctenaspis*, a new genus of cyathaspidian fishes; a preliminary report. Skr. om Svalbard og Ishavet, **33**: 1–7, 4 figs.

1932. The Downtonian and Devonian vertebrates of Spitsbergen. IV. Suborder Cyathaspida. (Posthumous; edited by A. Heintz). Skr. om Svalbard og Ishavet, **52**: 1–26, 11 pls., 12 figs.

Kiaer, J., and A. Heintz

1935. The Downtonian and Devonian vertebrates of Spitsbergen. V. Suborder Cyathaspida. Part I, Tribe Poraspidei, Family Poraspidae. Skr. om Svalbard og Ishavet, **40**: 1–139, 40 pls., 57 figs.

Kunth, A.

1872. Ueber *Pteraspis*. Zeitschr. Deutsch. Geol. Ges., **24**: 1–8, Taf. 1.

LINDSTROEM, G.

1895. On remains of a *Cyathaspis* from the Silurian strata of Gotland. K. Svenska Vet.-Akad, Handlingar, **21**, Afd. 4, No. 3: 1–15, 2 pls.

MATTHEW, G. F.

1886. A preliminary notice of a new genus of Silurian fishes. Bull. Nat. Hist. Soc. New Brunswick, **6**: 1–5, 1 fig.

1886. Discovery of a pteraspidian fish in the Silurian rocks of New Brunswick. Canadian Records of Science, **2**, no. 4: 242–252, 1 fig.

MOY-THOMAS, J. A.

1939. Palaeozoic fishes. 148 pp., 31 figs. London.

PAUCA, M.

1941. Poissons paléozoiques de la rive bucovinienne du Dniester. C. R. Inst. Geol. Roumanie, **26**: 14–31, 2 pls., 4 figs.

ROMER, A. S.

1945. Vertebrate paleontology. 687 pp. Chicago.

RUEDEMANN, R.

1916. Spathiocaris and the Discinocarina. Bull. New York State Mus., **189**: 98–112, pl. 32.

1920. A recurrent Pittsford (Salina) fauna. Bull. New York State Mus., **219**, **220**: 205–222.

STRAND, E.

1934. Zoologische und paläontologische Ergebnisse von den Svalbard- und Eismeer- Untersuchungen Norwegens. Folia Zool. Hydrobiol., **5**: 326–330.

VASCAUTANU, T.

1931. Les formations siluriennes de la rive roumaine du Dniester. Ann. Inst. Geol. Roumanie, **15**: 585–661.

WHITE, E. I.

1935. The ostracoderm *Pteraspis* Kner and the relationships of the various agnathous vertebrates. Phil. Trans. Royal Soc. London, (B), **225**: 381–457, pls. 25–27, 97 figs.

WHITE, E. I., and J. A. MOY-THOMAS

1940–1941. Notes on the nomenclature of fossil fishes. I. Homonyms A-C. Ann. Mag. Nat. Hist., **5** (1940): 502–507. II. Homonyms D-L. *Ibid.*, **6** (1940): 98–103. III. Homonyms M-Z. *Ibid.*, **7** (1941): 395–400.

WHITLEY, G. P.

1940. The Nomenclator Zoologicus and some new fish names. Australian Naturalist, May, **1940**: 241–243.

WILLS, L. J.

1935. Rare and new ostracoderm fishes from the Downtonian of Shropshire. Trans. Royal Soc. Edinb., **58**: 427–447, 7 pls., 4 figs.

WOODWARD, A. S.

1889–1901. Catalogue of fossil fishes in The British Museum, 4 vols. London.

1934. Note on a new cyathaspidian fish from the Upper Downtonian rocks of Corvedale. Quart. Jour. Geol. Soc. London., **90**: 566–567, 1 pl.

PLATE 1

Vernonaspis allenae, n. sp.

Dorsal plate, x 5½, holotype. Note surface detail and exfoliation of plates on anterior lateral region, where are shown outlines of a small anterior lateral plate with a smooth interior, and behind it a second lateral plate with an internal polygonal pattern. The apparent sharp line separating the rostrum from the central disc is clearly a crack and not an original feature.

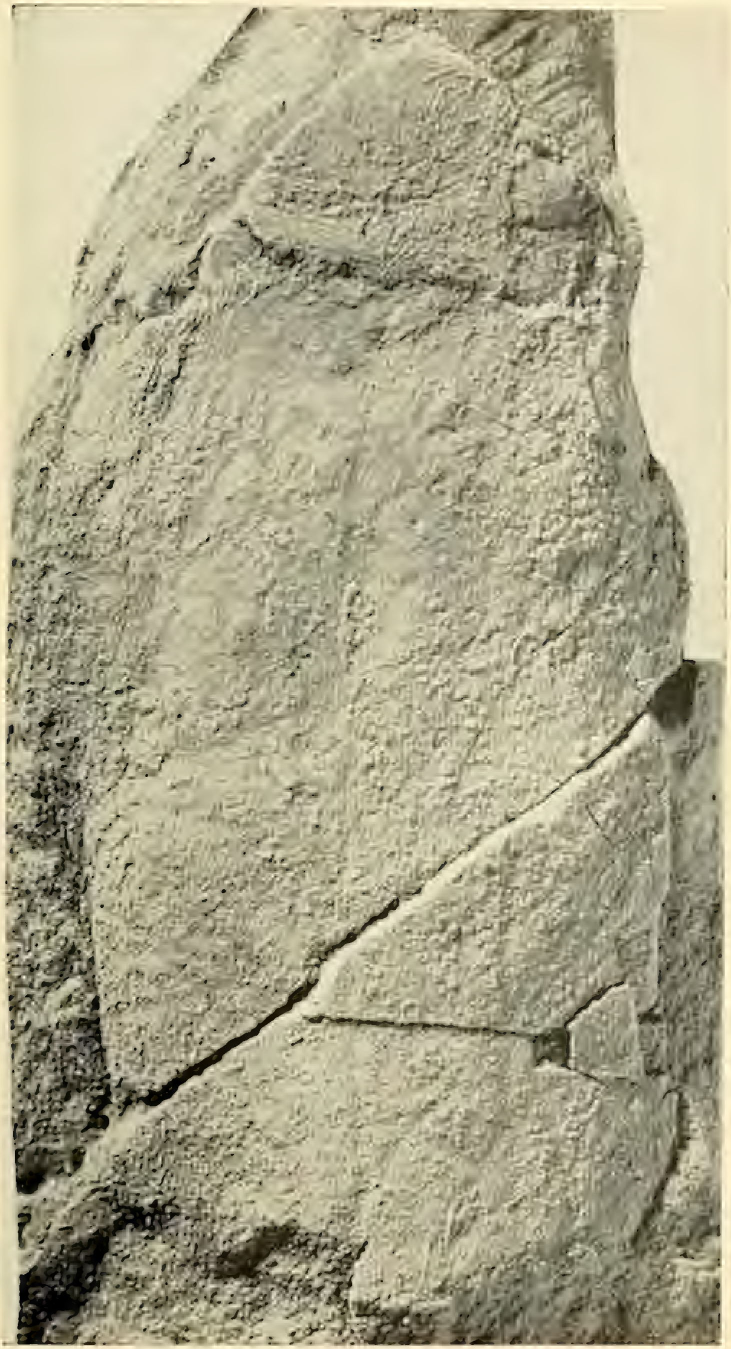


PLATE 2

1–2. *Archegonaspis drummondi* n. sp.

Holotype, an internal impression of a dorsal plate, x2. (1) whitened, (2) natural color.

3. *Vernonaspis allenae* n. sp.

Rubber impression from external mold of holotype, x7, showing a portion of the surface pattern over the lateral plates, which bear longitudinal lines, making these plates inconspicuous externally. Same specimen as Plate 1.

4. *Cyathaspis "wardelli"* of Bryant.

Longwood shale, Shin Hollow, near Port Jervis, New York. x2. New York State Museum.

5. *Cyathaspis wardelli*

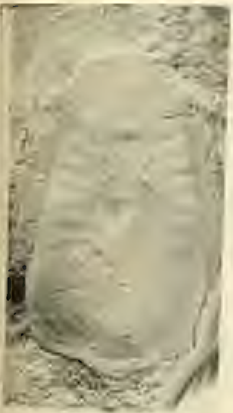
Lectoholotype, a probable branchial plate, x2. New York State Museum, no. 9613.

6–7. *Vernonaspis leonardi* n. sp.

Ventral plate tentatively assigned to this species. (6) Internal mold, natural color, showing traces of cancellous layer; (7) whitened, showing form more clearly, also faint cracks and possible traces of canals. See also text figure 1.

8. *Vernonaspis allenae* n. sp.

Holotype, x2, showing more clearly than the enlargement on Plate 1, grooves of a possible lateral line system complicated by wrinkles of no organic significance.



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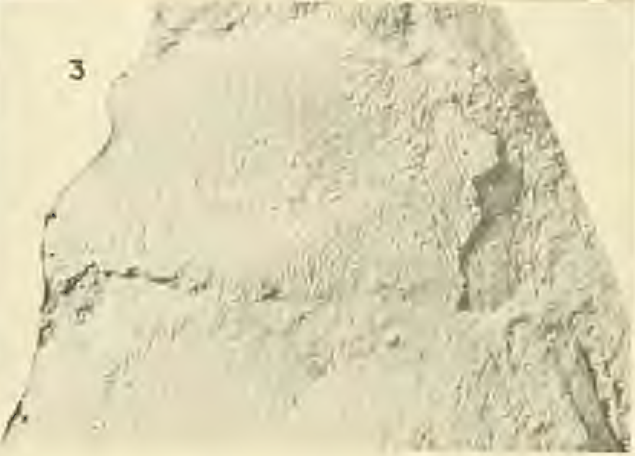

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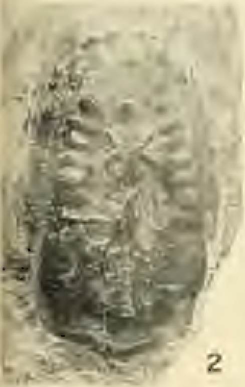

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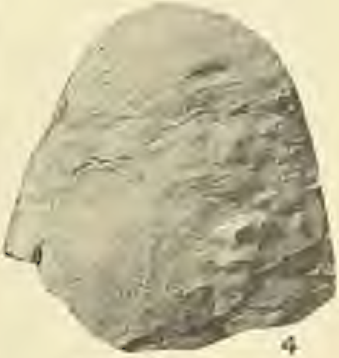

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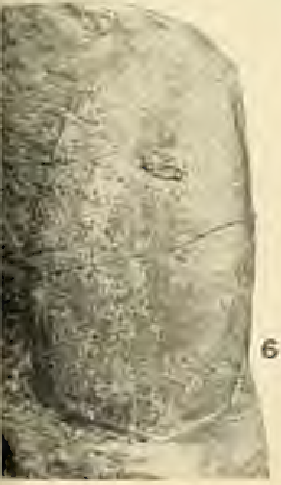

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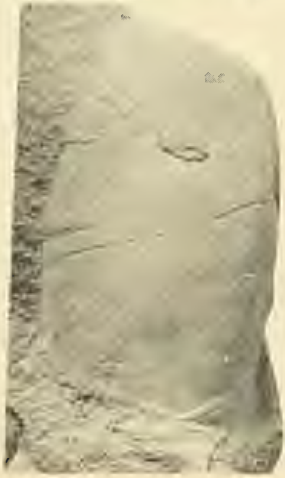

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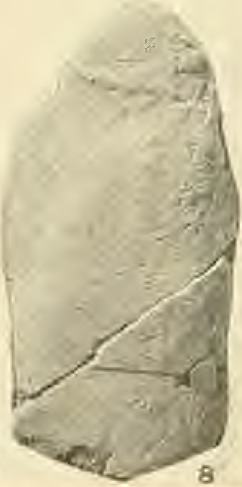

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PLATE 3

1. *Cyathaspis wardelli* (Ruedemann)

Syntype, a fractured branchial plate. New York State Museum no. 9618.

2–4. Cf. *Vernonaspis leonardi*

(2) Interior of dorsal plate. (3) Impression of same, showing more clearly pineal body, branchial impressions, semicircular canals, and impression of brain. (4) Rubber mold from interior shown in figure 2, showing more clearly the posterior margin of the plate.

5. *Vernonaspis leonardi*

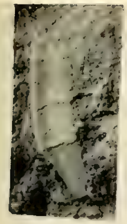
Rubber impression from external mold of anterior end of dorsal plate, showing nature of ornament of dentin ridges. x7.

6. *Archegonaspis* ? sp.

Interior of ventral plate, natural color, after etching, exposing canals of lateral line system, shown more clearly in Plate 8, figure 3, and some surface features of the dentin ridges. See also text figure 2.

7. *Cyathaspis wardelli* (Ruedemann)

An incomplete dorsal plate. Syntype. New York State Museum no. 9617. x2.



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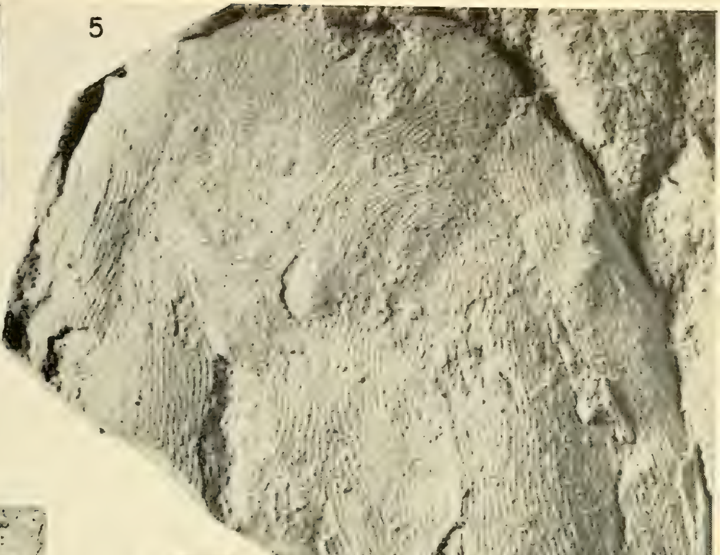

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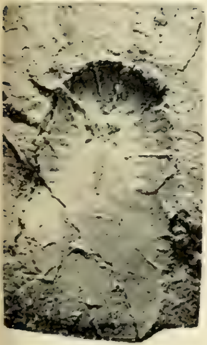

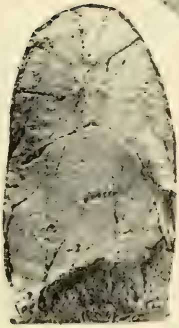

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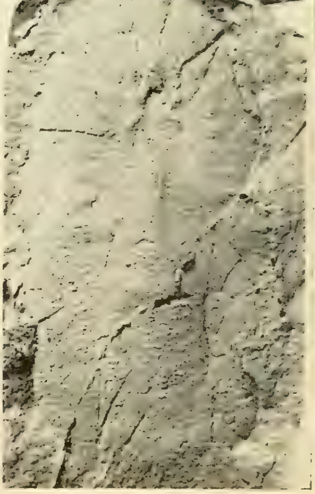

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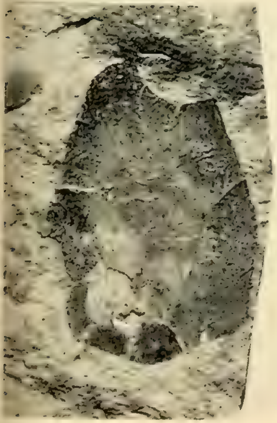

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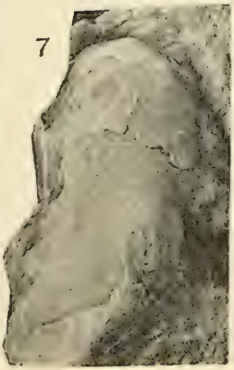

PLATE 4

Cf. *Vernonaspis leonardi*

Interior of dorsal plate, x4, showing in natural color, the pattern of the cancellous layer, and the posterior margin with dentin layer only. See also Plate 3, and Plate 5, figure 1.

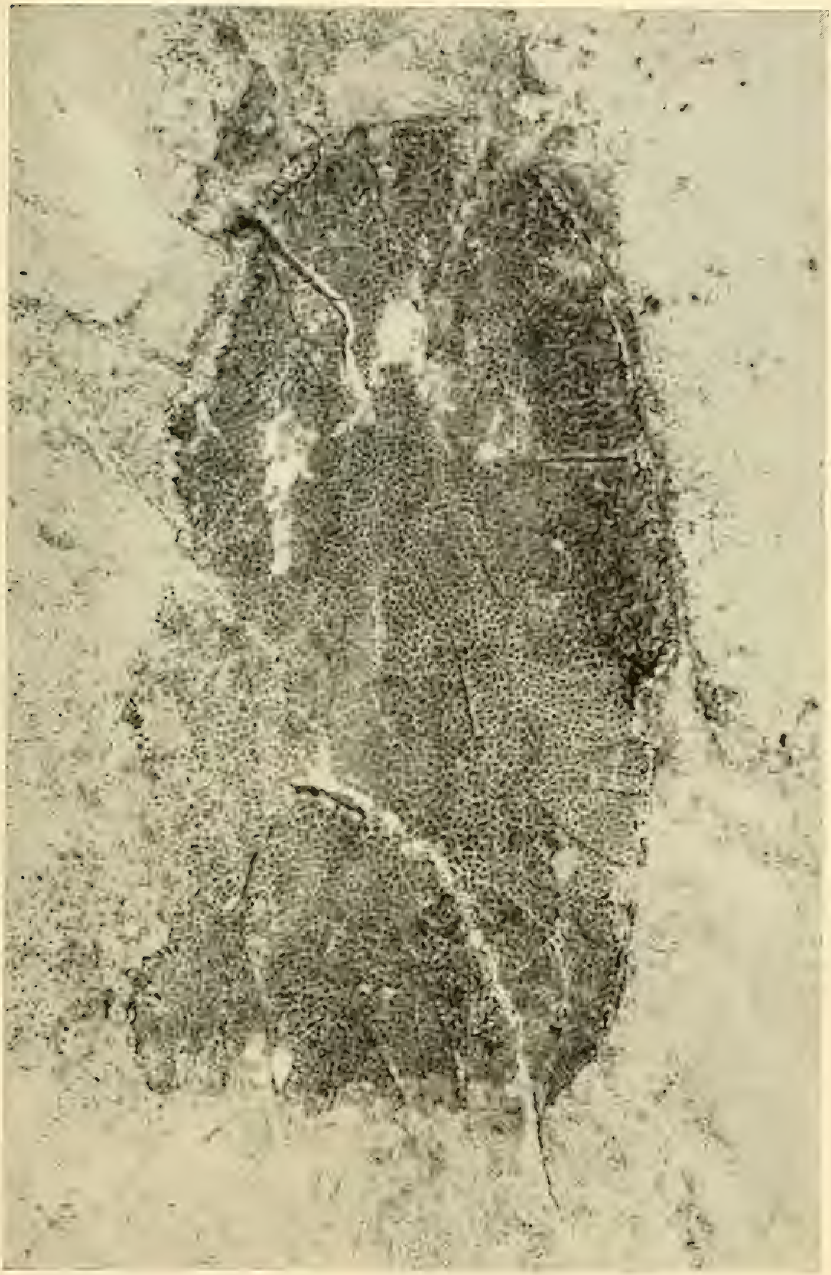

PLATE **5**

1. Cf. *Vernonaspis leonardi*

Broken edge of dorsal plate shown in Plate 4, showing traces of layers. x16.

2. *Vernonaspis leonardi* n. sp.

Rubber impression from external mold of ventral plate, from same specimen as that shown as an internal mold on Plate 2, figures 6 and 7.

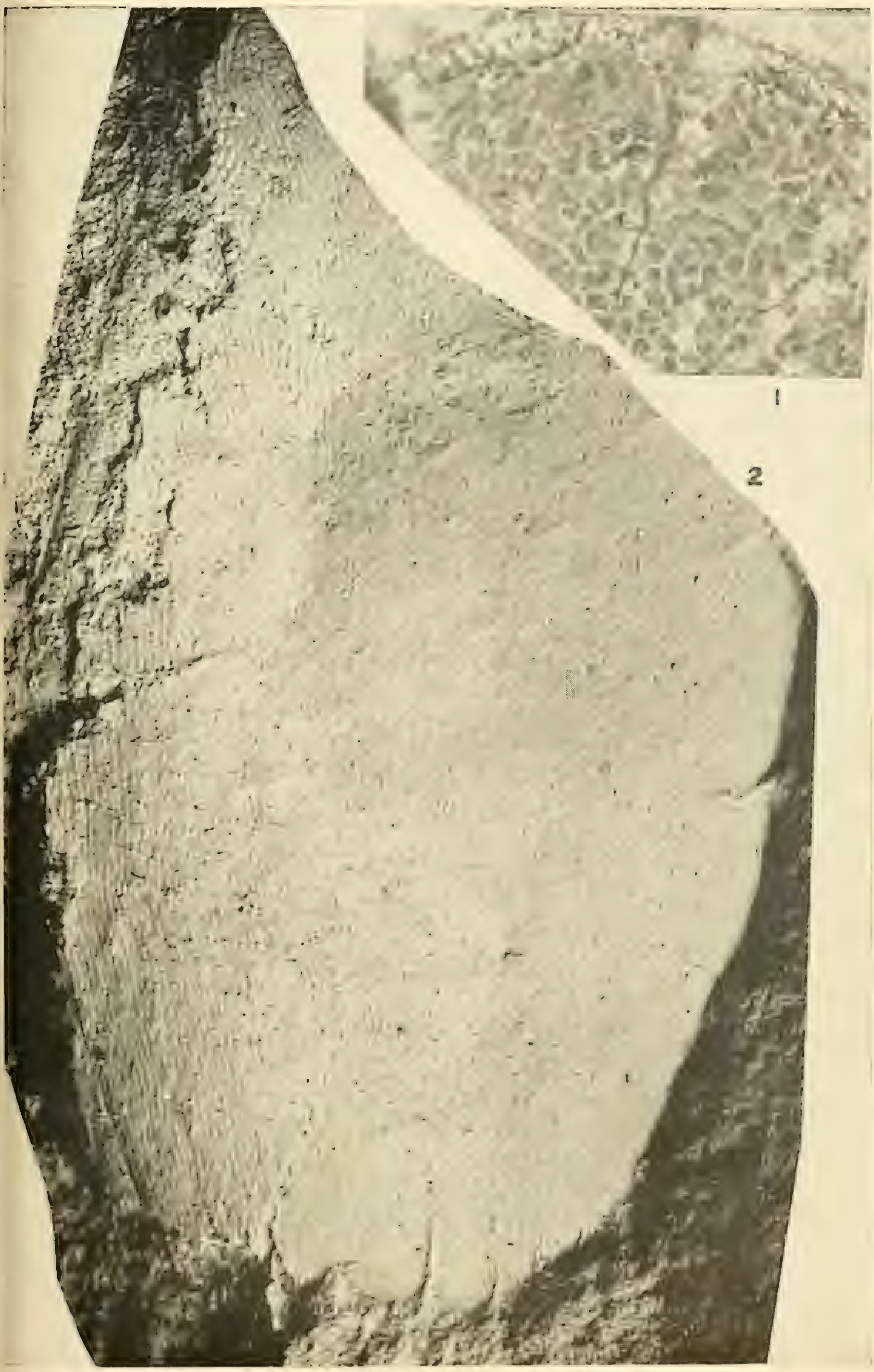
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PLATE 6

Archegonaspis cf. drummondi

Rubber impression from external mold of ventral plate tentatively assigned go this species, showing anterior end with pattern characteristic of *Archetonaspis.*

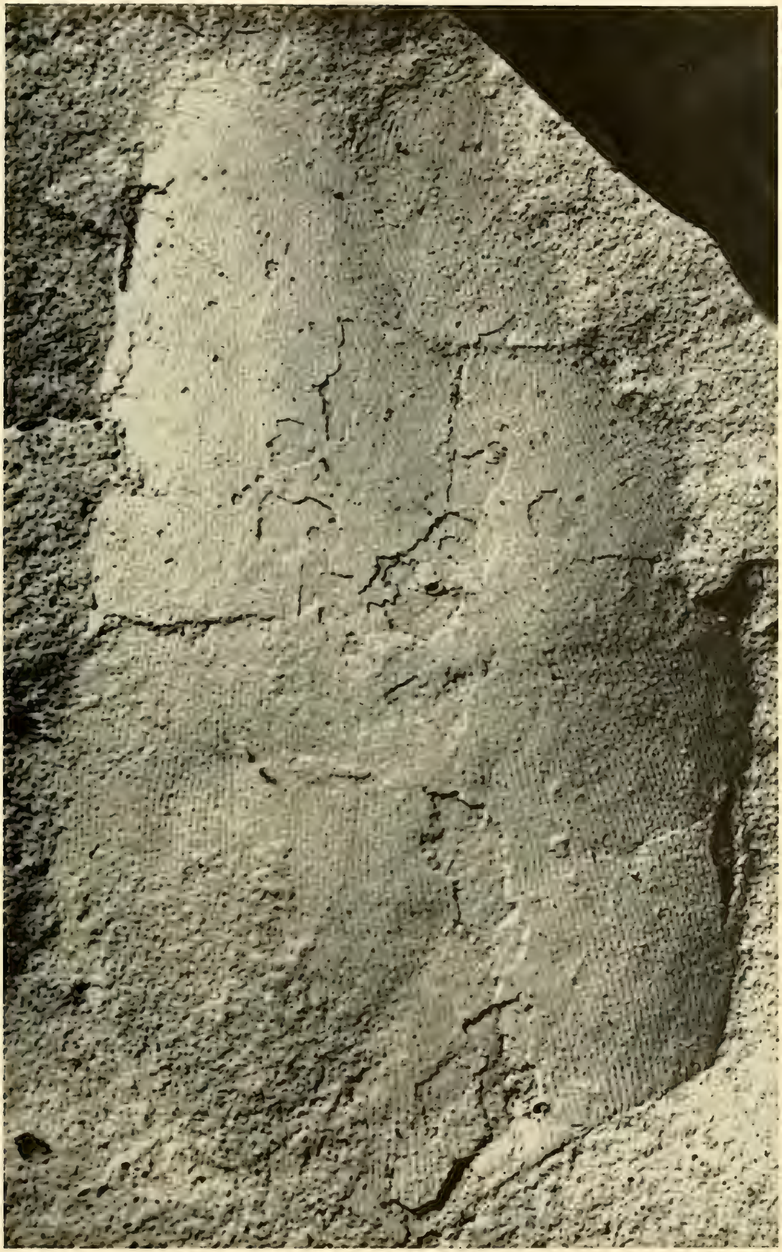

PLATE 7

Archegonaspis ? sp.

Interior of ventral plate, whitened, etched, showing cancellous layer and the interrupted canals of the lateral line system, also in places, penetrating to the dentin layer. In the lower left quadrant the plate is removed completely, showing the external mold of the pattern of the dentin layer; note that the grooves do not appear to be as deep in this portion. See also Plate 3, figure 6, and Plate 8, figure 3, and text figure 2.

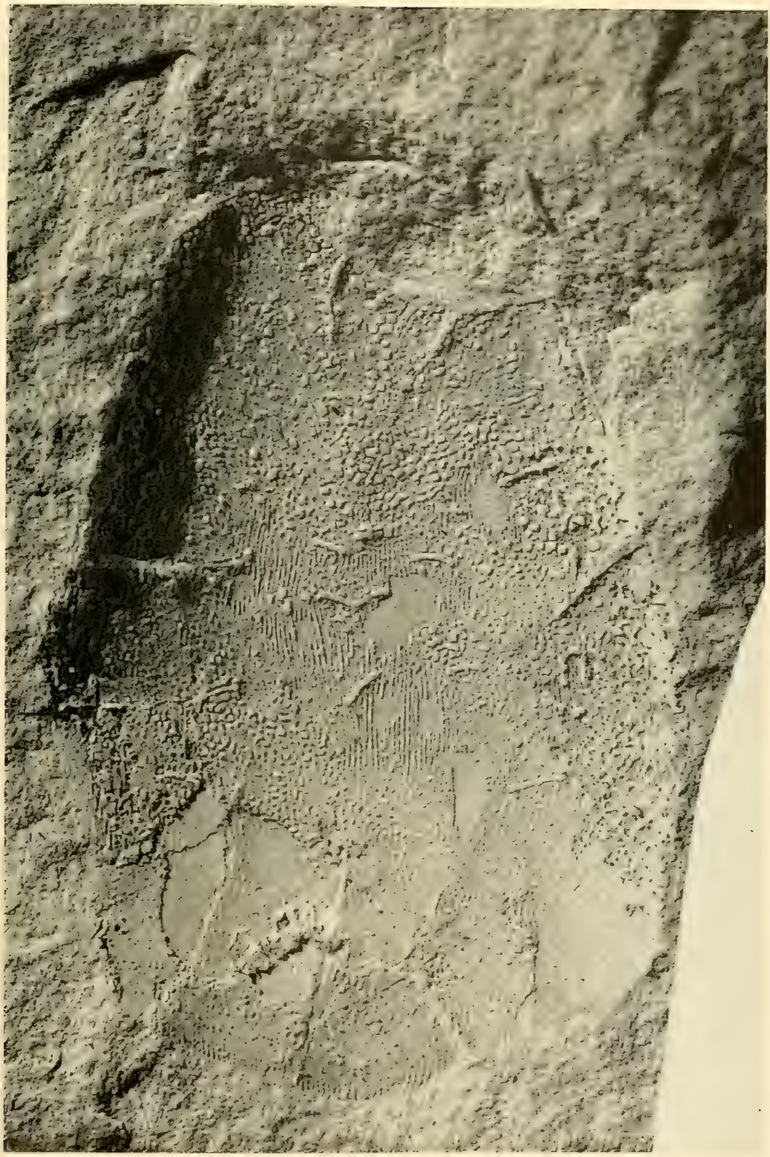

PLATE 8

1–2. Branchial plate of unknown taxonomic affinities. x2. (1) whitened; (2) natural color.

3. *Archegonaspis* ? sp.

Internal impression of ventral plate. Same specimen as Plate 7, and also Plate 3, figure 6 and text figure 2.

1

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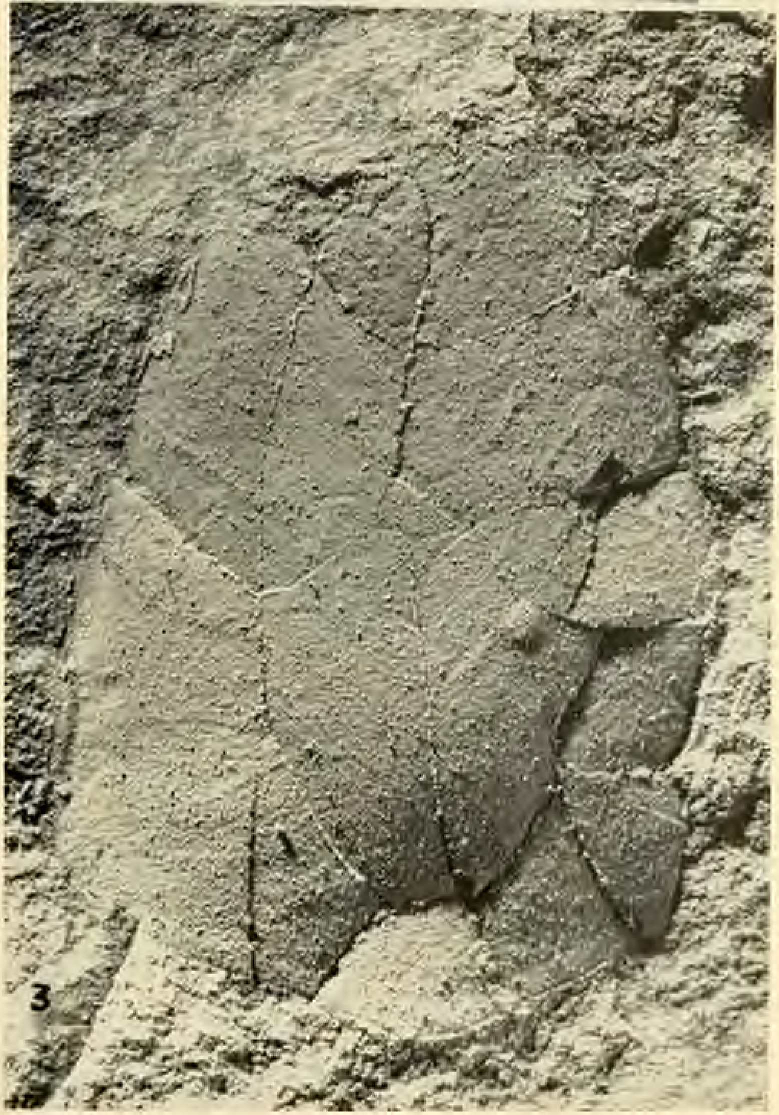
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Bulletin of the Museum of Comparative Zoology
AT HARVARD COLLEGE
Vol. 107, No. 7

NOTES ON SOME PETRELS OF THE NORTH PACIFIC

By Oliver L. Austin, Jr.

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM
November, 1952

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NOTES ON SOME PETRELS OF THE NORTH PACIFIC

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No. 7.—*Notes on Some Petrels of the North Pacific.*

By Oliver L. Austin, Jr.

In the course of preparing a comprehensive work on the birds of Japan[1] it has been necessary to review the extra-limital forms of several genera of Tubinares. As the results of this study are of significance in other areas, they are presented here instead of being held for inclusion in the work on Japan now in progress.

The Tubinares, particularly the smaller species, are a difficult group systematically because of their relatively slight morphological variation. Many of the populations occupy restricted but widely separated breeding grounds, to which it may be assumed they show a high degree of individual site tenacity. The group being an ancient one, some of the present breeding colonies may have been occupied continuously since late Tertiary time, possibly longer. Yet despite wide geographical separation, the birds have all existed under such similar ecological conditions that no structural modifications have been encouraged, and only minor fortuitous changes have been perpetuated genetically.

The recognition of geographical populations by their slight morphological differences can be of great importance, particularly in the petrels which wander so far over the trackless seas in the non-breeding season. Other than by extensive banding on the breeding grounds, the year-round movements and distribution of the various breeding populations can be learned only by the ability to assign to their proper nesting grounds all the specimens taken away from them. Systematic study of the geographical races of petrels has been hampered by the paucity of comparable specimen material, which must be taken on the breeding grounds and be of similar age, both of the individual when collected and of the specimens themselves. The problem is aggravated by a bewildering synonymy, a plethora of names given to minor variations shown by small, inadequate series, and in some cases on geographical grounds alone. The group has been attacked and mutilated by some of the most liberal and radical of splitters, and studied as well by some of the soundest and most conservative systematists.

No one relishes being considered either an unscrupulous "splitter"

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[1] Financed in part by a J. S. Guggenheim Memorial Foundation Fellowship.

or an unconscionable "lumper", but at the moment my tendencies seem, in common with the general trend, to lean toward the latter and the "conservative right". A subspecific name designating a geographical population is of no practical use unless at least three-quarters or more of the individuals of that population can be identified correctly by their morphological characteristics alone. The recognition of variations in color is still largely a matter of individual ability, integrity, and judgment because we have yet to find a satisfactory method of measuring color accurately. For mensurable characters such as size, the most practical standard is the statistical device (see Simpson and Roe, 1939) whereby two populations are considered separable only when the means of a given character in each population are as far or farther apart then the sum of their standard deviations. This allows the separation of at least 84 per cent of each population from 84 per cent of the other. Among the petrels it is rare indeed to find the means of any character separated by two standard deviations, allowing a 97 per cent separation.

Many of the named petrel races have been described, despite almost complete overlap, on claimed "average" differences. Statistically these "average" differences are of no significance unless it can be demonstrated that two standard errors on either side of the respective means do not overlap, and even then it is not possible to identify individual specimens with any degree of confidence. It may eventually be desirable to name these "average" populations, but for present purposes I can see no practical value in a name unless it can be applied with assurance, and without reference to the collecting data on the specimen's label. In this study I have adhered as closely as possible to the "84 per cent from 84 per cent" convention.

Genus PTERODROMA — the Gadfly Petrels

The only members of this genus in the northwest Pacific belong to the difficult group separated by Mathews (1934b, 169) into the genus *Cookilaria,* but which Murphy (1929 and 1936) lumps with *Pterodroma* and divides into two species and ten subspecies. A more natural division of the ten recognized races both morphologically and geographically is into three species. I propose revising Murphy's key to the genus (1929, 2) as follows:

A.1. Crown and nape close to a "neutral gray" and concolor with the back:

1. *Pterodroma cookii cookii* (New Zealand)
2. *Pterodroma cookii axillaris* (Chatham Islands)
3. *Pterodroma cookii nigripennis* (Kermadec Islands)
4. *Pterodroma cookii orientalis* (breeding grounds unknown)
5. *Pterodroma cookii defilippiana* (Masatiera Id., Juan Fernandez)

A.2. Crown and nape mainly sooty black, much darker than the back, with which it forms a sharp contrast:

B.1. Inner web of outer primaries with a wedge-shaped white patch extending at least half the distance of the feathers from the base:

1. *Pterodroma leucoptera leucoptera* (east Australia and nearby islands)
2. *Pterodroma leucoptera masafuerae* (Masafuera Id., Juan Fernandez)
3. *Pterodroma leucoptera longirostris* (breeding grounds unknown)

B.2. Primaries wholly dark, with no white on inner webs:

1. *Pterodroma brevipes brevipes* (New Hebrides and Fiji Ids.)
2. *Pterodroma brevipes hypoleuca* (Hawaiian and Bonin Ids.)[1]

Pterodroma cookii does not occur in the northwest Pacific. *Pterodroma leucoptera* is represented there only by the rare and little-known *P.l.longirostris* which, though described originally from Mutsu Bay in northern Honshu, Japan, will probably be found eventually to nest in southern seas and to occur in the north Pacific only as a migrant. This form is still known only from ten specimens: Stejneger's type and cotype in the Yamashina Museum, Tokyo; two undated Owston skins from the type locality in the American Museum of Natural History in New York; and the six specimens in the Chicago Museum of Natural History taken at sea by the Crane Expedition on 17 August 1929 about 600 miles east of the type locality (cf. Murphy 1930, 14–15).

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[1] It is extremely unlikely that Krusenstern Island, the type locality of *hypoleuca* (and also of Salvin's *Puffinus cuneatus*) is Ailuk in the Marshall group as stated by Fisher (1946, 588). According to Baker (1951, 65, 70), who nevertheless accepts Fisher's hypothesis, the only Micronesian records for *Pterodroma brevipes hypoleuca* and *Puffinus pacificus cuneatus* are the type specimens of each from the mysterious "Krusenstern". It is far more likely, as James C. Greenway, Jr. first pointed out to me in 1948, that when Captain H. J. Snow collected these specimens he was engaged on a feather raid at Laysan where both species are common, and used the mythical and unlocatable Krusenstern on the labels of the skins he sent back to England to hide the scene of his activities from the authorities and from his competitors. At Mr. Greenway's suggestion I searched in Japan for records of the old Yokohama firm of Owston and Snow, which might supply a clue to the island's identity, but no former associate of the firm is alive today, and any of its records that might have existed prior to the war were destroyed by the fire raids of 1945. The question can never be answered with certainty, but Mr. Greenway's logical hypothesis was accepted by Murphy (1951, 18) for the type locality of *cuneatus*. The type locality of Salvin's *Œstrelata hypoleuca* is hereby designated as Laysan Island in the Hawaiian group.

Pterodroma brevipes breeds in the Hawaiian, Bonin, Fiji, and New Hebrides islands. No color differences have been ascribed to any of these populations, nor have I been able to discern any in the series I have examined. As suspected by most authorities from the few specimens previously available, an adequate series of *brevipes* from Japan and the Bonin Islands proves indistinguishable in measurements from the Hawaiian population, *P.b.hypoleuca* (table 1, fig. 1). However, the southern population of the Fijis and New Hebrides is separable from the populations of Hawaii and the Bonins on the basis of its smaller dimensions (table 1, fig. 1), particularly in the tail, to a lesser extent in the wing and culmen. The type of *brevipes* in the U. S. National Museum unfortunately has the longest tail in the series of southern birds, 109 mm., but the cotype's tail (also in the U. S. Nat. Mus.) measures only 94 mm. The exact collecting locality of these two birds is doubtful (cf. Murphy, 1929, 15), but the name is valid both for the species and the southern race.

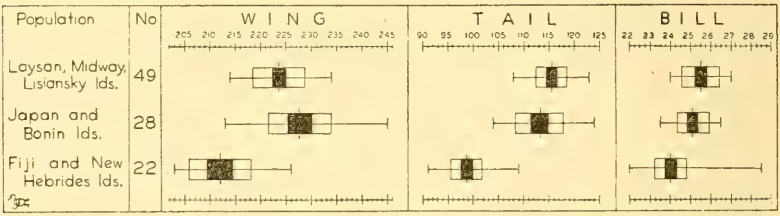

Fig. 1. Measurements of *Pterodroma brevipes* populations from Table 1 graphed in the form of Hubbs-Perlmutter diagrams. In each diagram the solid horizontal line represents the observed range of variation, the central vertical line represents the mean, the rectangle indicates one standard deviation to either side of the mean, and the black part of each rectangle indicates twice the standard error of the mean. (For a discussion of the use of this method to demonstrate differences and similarities between populations see Hubbs and Perlmutter, 1942.)

Genus OCEANODROMA — Storm Petrels

The Storm Petrels have a strong claim to the dubious honor of being one of the most difficult systematically of avian groups. Their morphological differences are in many cases so slight that many forms of specific rank cannot be identified with certainty in the field, and some of them only with difficulty in the hand. Representative populations of some species, though oceans apart geographically, can be told apart if at all only by average measurements which allow fewer than half the individuals to be identified with assurance.

The characters used are size and color. Size variation is very slight, and color is frequently even less definitive and reliable. The various shades of black employed by many students of the group are deceptive and misleading. They vary within populations with the time of year or state of molt of the individual, and particularly with the age of the specimen. The lead "bloom" characteristic of several forms fades and foxes with age, both of the individual in life and of the museum specimen. Nevertheless color is a valid character, and in some cases more definitive than measurements, even though the differences can sometimes be seen only with a series of fresh specimens in the hand and in good light.

As I have been concerned with only three aggregations of this complex society of small black sea birds, I do not feel qualified to judge the larger systematic relationships of the group as a whole. Several of its elements have been separated as distinct genera, but under the present tendency to use the genus as a collective rather than a distinctive category, I believe it best to regard them all as congeneric. Nor does the establishment of subgenera seem warranted, though several of them combine into well-defined "species groups".

OCEANODROMA CASTRO — Madeiran Fork-tailed Petrel

This is one of the most wide-spread but least variable of the small black petrels. A small, white-rumped species, it is distinct from the other similarly colored and dimensioned species only in the shallower forking of its tail and in having the white rump feathers broadly tipped with black. Neither of these characters can be discerned without having the bird in the hand. It breeds in both hemispheres in widely-separated island colonies. Each of the known breeding populations has been named on minor color and size differences, and the synonymy is a long one.

I can find no valid color differences in the material I have examined, none that are not ascribable to age-foxing or seasonal wear and fading. Each population exhibits minor size differences, but figure 2 and table 2 show the futility of trying to assign any but a few extremes among the available specimens to their proper populations on measurements. Some of the series I have measured are admittedly small (though much larger than those used by the describers of all but the proposed Atlantic races), but they are adequate by the tenets of modern statistical analysis. Not only is the overlapping almost complete, but there is no significant difference in their means, and larger series will undoubtedly show even slighter average differences. None of the proposed subspecies is tenable, and systematically the species is indivisible.

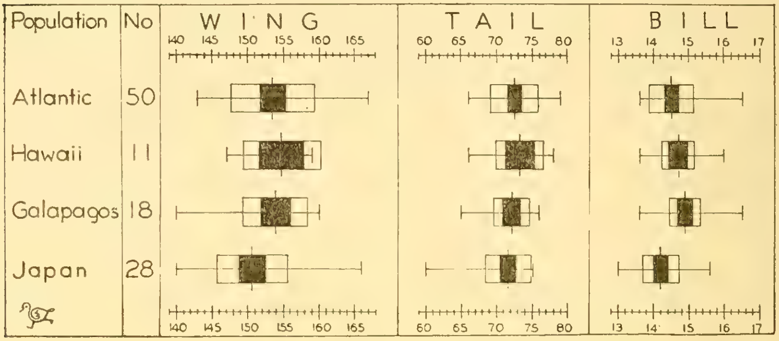

Fig. 2. Diagrammatic presentation of measurements of *Oceanodroma castro* populations from Table 2.

The MELANIA-MARKHAMI-TRISTRAMI-MATSUDAIRAE complex

Limited to the Pacific are four very similar forms of puzzling and ambiguous systematic relationship. They are the largest of the small, fork-tailed storm petrels, remarkably similar in size, and all are black-rumped. Two of them, *markhami* and *melania*, occur only in the eastern Pacific; the other two, *tristrami*[1] and *matsudairae*[2] only in the central and western. Hitherto they have been regarded tentatively as two subspecies respectively of two species, *tristrami* as a race of *markhami*, and *matsudairae* of *melania*. I consider them equally of specific rank, and key them as follows:

---

[1] When they described *Cymochorea owstoni*, Mathews and Iredale (1915, 581) discarded *tristrami* as of doubtful identity, in which they have been followed by Hartert (1915, 1415) and the Ornithological Society of Japan Special Committee (Hand-List 1942, 135). Although the type of *tristrami* was lost, the descriptions of it by Salvin in his "Key to the Species" of *Oceanodroma* (1896, 347) where the name *tristrami* is first mentioned, and by Ridgway in Salvin (*idem*, 354–355) are clearly identifiable in the light of the more adequate material now available. Three of the characters given are diagnostic, the tarsus length, the "plumbeous" color of the head and mantle, and particularly the light edgings of the tertials and wing-coverts. Coupled with the Sendai Bay type-locality (the bird is fairly common in those and adjacent waters, and none of the three similar forms with which it might be confused has ever been taken in northeastern Honshu), they leave no doubt whatever as to which form the name must be applied. I have examined the type of *owstoni* which, as suspected by Peters (1931, 74, footnote), is unquestionably a synonym of *tristrami*.

[2] Mis-spelled *matsudariae* in the origenal description (Kuroda 1922, 311),but named in honor of Marquis Matsudaira, the first serios student of the patrels in Japan. The original spelling is here-corrected.

A.1. Tarsus 30 mm. or more:
    O. melania (breeds on islands off southern and Baja California.)
A.2. Tarsus less than 30 mm.:
  B.1. Primary shafts white at base, no lead bloom on head and shoulders:
      O. matsudairae (breeds in the Bonin Islands.)
  B.2. Primary shafts dark at base, a lead bloom on head and shoulders:
    C.1. Tarsus less than 25 mm., wing bar poorly marked:
        O. markhami (breeding ground unknown, perhaps in the southern Peruvian or northern Chilean Andes [Murphy, *in lit.*]. The one egg known was taken from a bird shot off central Peru.)
    C.2. Tarsus 25 mm. or more, the upper secondaries and tertials lighter at the tips, forming a distinct wing bar:
        O. tristrami (breeds in the Bonin, southern Izu [Torishima], and Hawaiian [Laysan] islands.)

Table 3 and figure 3 show the average and inclusive measurements of the specimens examined. Although all four species show average differences, their dimensions overlap so that they are of diagnostic

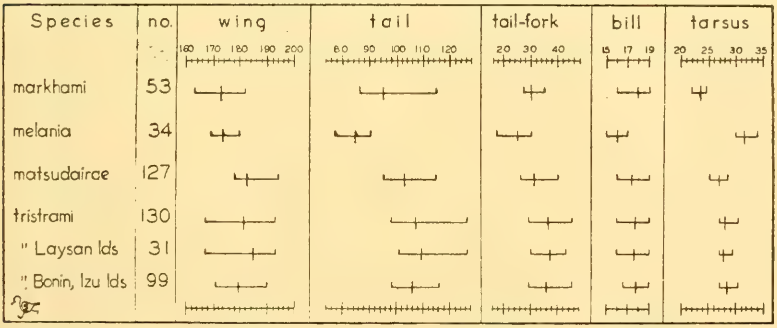

Fig. 3. Average and inclusive measurements of the Black Fork-tailed Petrels from Table 3.

value only in *melania* and *markhami*. *O. melania* has a longer tarsus with practically no overlap, and a shorter bill, tail, and tail fork than any of the other three forms, though the latter three characters have too much overlap to be of much value. *O. markhami* is distinct in having the shortest tarsus of the four.

Color differences are of more use in separating the four forms. The heads and shoulders of *markhami* and *tristrami* in fresh plumage show a pronounced lead-gray bloom which is lacking in the uniformly brownish-black *melania* and *matsudairae*. The bloom fades with time, however, so that old specimens of *tristrami* can be told from *matsudairae* only by the color of the primary shafts which in the latter are uniquely white at the base when viewed dorsally, less so ventrally. *O. tristrami* is distinctive in the light margins of the upper secondary and tertial coverts, which form a pronounced light wing patch. The differences and similarities of the four forms may be tabulated as follows:

	Tarsus	*Primary shafts*	*Heads and shoulders*	*Wing patch*
melania	30–34.5 mm.	dark	brownish	not pronounced
matsudairae	25–28.5	light	brownish	not pronounced
markhami	22–25	dark	lead gray	not pronounced
tristrami	26–30.5	dark	lead gray	pronounced

Only in the presence or absence of the lead bloom on the heads and shoulders do the four species divide themselves into two equal groups with one representative of each on each side of the Pacific. Each form otherwise has its own distinctive characteristics not shared by the other three: *melania* its long tarsus, *markhami* its short one, *matsudairae* its light primary shafts, *tristrami* its light wing patch. *O. tristrami* and *matsudairae* are unquestionably specifically distinct, because they breed sympatrically in the same colonies in the Bonin Islands. Although the breeding place of *markhami* is unknown, neither it nor *melania* so far as known is sympatric with the other or with either of the two western forms. Hence either or both might be conspecific with either *tristrami* or *matsudairae*. We have only external morphological characters to go by, and these are neither indicative nor salient. Actually there is no way of determining the relationships of these allopatric forms other than arbitrarily, and until better evidence is available of their possible subspecific affinities, all four are best regarded taxonomically as of full specific rank. They have all doubtless evolved from a common ancestor, and form a fairly tightknit "species group" in the genus *Oceanodroma.*

On the strength of its long tarsus, Mathews (1934a, 119) proposed placing *melania* in the monotypic genus *Loomelania,* in which he has been followed by Murphy (1936, 744). I cannot see that this is warranted, or accomplishes any nomenclatural improvement, for the short tarsus of *markhami* and the white primary shafts of *matsudairae* make them just as worthy (or unworthy) of generic rank.

Figure 3 also shows by an adequate series of measurements that the two widely separated populations of *tristrami,* one on Laysan Island and the other on the Bonins and southern Izus, are inseparable.

OCEANODROMA LEUCORHOA — Leach's Fork-tailed Storm Petrel

This complex of small, fork-tailed petrels breeds in the northern hemispheres of both the Atlantic and the Pacific. Most authorities agree that the populations of the Atlantic and of the northwest Pacific are inseparable, and recognize the northeastern Pacific population,

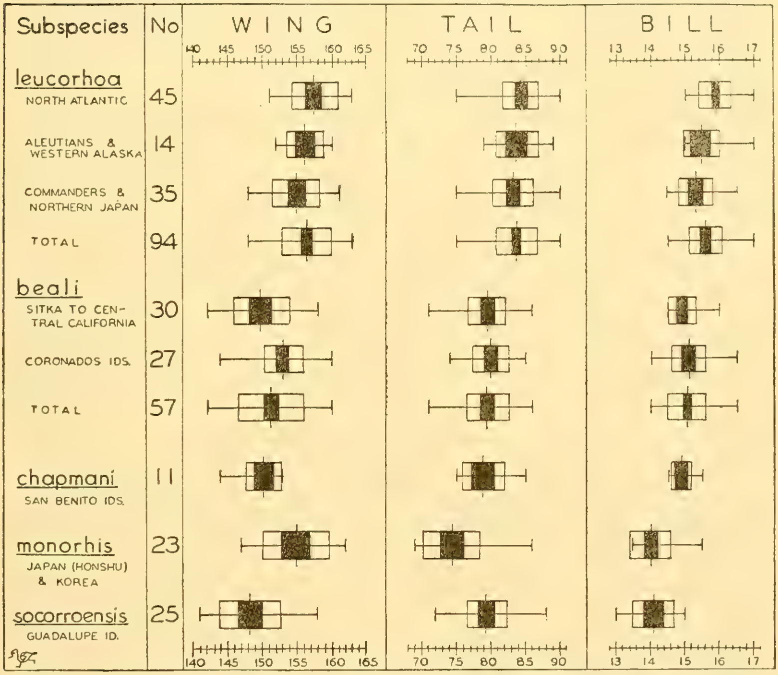

Fig. 4 Diagrammatic representation of measurements of *Oceanodroma leucorhoa* populations from Table 4.

O. l. beali, as smaller, and forming a cline in the variability of the white rump patch as it progresses southward on the west coast of North America, reaching its climax in the black-rumped population of San Benito Island, *O. l. chapmani.* As yet no harmony has been attained in the number of intermediate forms to be recognized in the eastern Pacific.

In the western Pacific, breeding on islands off Honshu, Kyushu, and Korea, is another black-rumped population, *monorhis,* which has been considered specifically distinct, but which is distinguishable from the San Benito population only by slight measurements. No cline either in color or size has yet been demonstrated between *monorhis* and the white-rumped *leucorhoa* population breeding on islands off northern Honshu and Hokkaido, though the latter shows some variability in the amount of white on the rump. In view of the cline between the white- and black-rumped populations in the eastern Pacific, and the fact that the Asiatic black- and white-rumped populations are allopatric, *monorhis* is best regarded as conspecific with *leucorhoa.*

Table 4 and figure 4 show how little difference exists in the measurements of the known populations of *leucorhoa* that have been studied and named. On dimensions alone these are all very weak races. Despite significant differences between the means of some characters, fewer than half of the individuals of many of the recognized subspecies are distinguishable. In the eastern Pacific, however, color can be used with size to advantage. As Loomis (1918) and van Rossem (1942) have pointed out, the white rump patch becomes darker from north to south, and the lead bloom of the upper parts fades to a browner black. The latter character varies with age of the specimen, the lead grays fading to brown in time just as they do in the previous group. This cline runs southward evenly from Sitka, Alaska, to the Farallon Islands off San Francisco, and breaks at Los Coronados Islands, the population of which is intermediate in color between the all-white-rumped birds to the north and the all-black-rumped birds to the south. None of these populations can be differentiated on size alone, and no sharp lines can be drawn between them in color. As none of the intermediate forms in the cline running from southern Alaska to Los Coronados Islands can be recognized, I synonymize both *beldingi* and *willetti* with *beali.*

The Guadalupe Island population, on the other hand, is quite variable in color, but distinctive in its small size. It is intermediate in its rump patch. Only one of the 23 Guadalupe specimens I have seen is entirely black-rumped, and the amount of white present in the remainder varies from four or five white feathers (as in the type of *socorroensis* which, as van Rossem pointed out (1942) is indeed the Guadalupe bird) to an intermediate condition with half the rump white, about as in the population of the central California coast.

From the material I have examined I believe the *O. leucorhoa* complex should stand as follows:

O. l. leucorhoa: Breeds on islands in the north Atlantic, and in the north Pacific from northern Japan (Hokkaido) through the Kuriles, Commanders, and Aleutians to islands off the west coast of Alaska. It is the largest of all in all measurements, and whitest in the rump patch.

O. l. beali: Breeds from southern Alaska (Sitka region) southward on islands off the west coast of North America to Los Coronados Islands off northern Baja California. Although their means are significantly smaller, on measurements only about half the population is distinguishable from *leucorhoa*. The rump patch varies from almost identical to that of the nominate form in the north, to absence in 50 per cent of Los Coronados population.

O. l. chapmani: Breeds on the San Benito Islands, off central Baja California. Indistinguishable from *beali* in size, but always with a black rump.

O. l. monorhis: Breeds on islands off southern Japan (Honshu and Kyushu) and Korea. Black rumped, and distinguishable from *chapmani* by its shorter bill. Its wing averages longer and its tail shorter than those of both *chapmani* and *socorroensis*.

O. l. socorroensis: Breeds on Guadalupe Island off Baja California. Distinguishable from all other races except *monorhis* by its smaller, slenderer bill. Rump patch variable, almost always with some white, but never as much as in typical *beali*.

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My thanks are also due to Dr. Herbert Friedmann for his courtesy in giving me access to the U.S.N.M. collections, and to Dr. R. C.

Murphy for his generosity not only in making available to me the excellent A.M.N.H. series of his own special group, but also for going over them with me, reading a draft of this paper, and making pertinent suggestions which I have been pleased to follow. Acknowledgements are made particularly to Nagahisa Kuroda, my collaborator in Japan, who measured for me the extensive series of petrels in the Japanese collections, and finally to Dr. J. C. Dickinson, Jr., for his assistance with the statistical methods employed.

BIBLIOGRAPHY

Baker, Rollin H.

1951. The avifauna of Micronesia, its origin, evolution, and distribution. Univ. Kansas Pub., Mus. Nat. Hist., **3** (1): 1–359.

Fisher, Harvey I.

1946. The type localities of *Puffinus pacificus cuneatus* Salvin and *Pterodroma leucoptera hypoleuca* (Salvin). Auk, **63**: 587–588.

Godman, F. DuCane

1907–1910. A monograph of the petrels. London, 376 pp., plates.

Hartert, Ernst

1912–1921. Die Vögel der paläarktischen Fauna. Berlin, vol. II, pp. i–xxiv+1764.

Hubbs, C. L., and A. Perlmutter

1942. Biometric comparison of several samples with particular reference to racial investigations. Amer. Nat. **76**: 582–592.

Kuroda, N.

1922. Remarks on the Japanese petrels of the genus *Oceanodroma*. Ibis, 1922, 309–314.

Loomis, L. M.

1918. A review of the albatrosses, petrels, and diving petrels. Proc. California Acad. Sci. (4), **2**, pt. 2, no. 12: 1–187, pls. 1–17.

Mathews, Gregory M.

1934a. A new genus of storm-petrels. Bull. British Ornithological Club, no. 376: 119.

1934b. A check-list of the Order Procellariiformes. Novitates Zool., **39**: 151–206.

———and T. Iredale

1915. On some petrels from the north-east Pacific Ocean. Ibis, 1915: 572–609.

Murphy, Robert Cushman

1929. On *Pterodroma cookii* and its allies. American Mus. Novitates, no. 370: 1–17.

1930. Diomedeidae, in Bds. Whitney Exp. XI. American Mus. Novitates, no. 419: 1–15.

1936. Oceanic birds of South America. Published by the American Mus. Nat. Hist., N.Y., vol. II: 642–1178.

1951. The populations of the Wedge-tailed Shearwater (*Puffinus pacificus*). American Mus. Novitates, no. 1512: 1–21.

Ornithological Society of Japan, Special Committee of the

1942. A hand-list of the Japanese birds. Tokyo, pp. i–viii+238.

Peters, J. L.

1931. Check-list of birds of the world. Cambridge (Mass.), vol. 1, pp. i–viii+306.

Salvin, Osbert

1896. Tubinares, in Catalogue of birds in the British Museum, vol. 25, pts. 3–8: 340–455.

Simpson, G. G., and A. Roe

1939. Quantitative zoology. N.Y. and London, McGraw-Hill, pp. i–xvii+414.

van Rossem, A. J.

1942. Preliminary comment on some Pacific Coast petrels. Proc. Biol. Soc. Washington, **55**: 9–12.

TABLE 1

Geographic variation in *Pterodroma brevipes*

(Measurements in millimeters)

Locality		Laysan, Midway, Lisiansky Ids.	Bonin Ids. & Japan	Fiji & New Hebrides Ids.
No. of specimens		49	28	22
Wing	Range	214–234	213–245	203–226
	Mean with standard error	229.6±.07	227.0±1.2	212.0±1.3
	Standard deviation	5.1	6.1	6.1
Tail	Range	108–123	104–124	91–109
	Mean with standard error	115.53±.49	113.13±.91	98.77±.63
	Standard deviation	3.1	4.8	3.06
Bill	Range	24.0–27.0	23.5–26.5	22.0–28.5
	Mean with standard error	25.5±.13	25.1±.15	24.02±.16
	Standard deviation	0.9	0.8	0.8

TABLE 2

Geographical variation in *Oceanodroma castro*

(Measurements in millimeters)

Locality		Atlantic colonies	Hawaii and Sandwich Ids.	Galapagos Islands	Japan
No. of specimens		50	11	18	28
Wing	Range	143–167	147–159	140–160	140–166
	Mean with standard error	153.46±.83	154.8±1.63	153.9±1.05	150.7±.92
	Standard deviation	5.9	5.4	4.5	4.9
Tail	Range	66–79	66–78	65–76	60–75
	Mean with standard error	72.46±.48	73.18±1.04	72.11±.59	71.64±.63
	Standard deviation	3.4	3.4	2.5	3.3
Bill	Range	13.6–16.5	13.6–16.0	13.6–16.5	13.1–15.6
	Mean with standard error	14.5±.09	14.7±.14	14.9±.11	14.2±.10
	Standard deviation	.64	.47	.47	.52

TABLE 3

Average and inclusive measurements in millimeters of the Black Fork-tailed Petrels

Species	No.	Wing	Tail	Tail Fork	Exposed Culmen	Tarsus
O. markhami	53	173.0 (163–182)	95.0 (86–105)	30.0 (27–35)	18.0 (16–19)	23.8 (22–24.5)
O. melania	34	173.4 (169–179)	84.5 (77–90)	24.9 (17–30)	16.0 (15–17)	31.3 (30–34)
O. matsudairae	127	184.2 (178–194)	103.0 (95–115)	31.9 (26–40)	17.3 (16–19)	26.8 (25–28 5)
O. tristrami	130	181.6 (167–193)	106.7 (98–123)	36.2 (29–45)	17.8 (16–19)	28.0 (27–30.[illegible])
,, ,, Laysan Id.	31	185.1 (167–193)	109.0 (101–123)	37.0 (30–43)	17.7 (16–19)	27.8 (27–29)
,, ,, Bonins, Izus	99	179.7 (171–190)	106.0 (98–116)	36.0 (29–45)	17.8 (16.5–19)	28.0 (27–30.5)

TABLE 4

Geographical variation in *Oceanodroma leucorhoa*

(Measurements in millimeters)

Subspecies		*Oceanodroma leucorhoa leucorhoa*				*Oceanodroma l. beali*			*O. l. chapmani*	*O. l. monorhis*	*O. l. socorroensis*
Locality		North Atlantic	Aleutians and western Alaska	Commanders and northern Japan	Total	Sitka to central California	Coronados Islands	Total	San Benito Islands	Japan and Korea	Guadalupe Island
Number of specimens		45	14	35	94	30	27	57	11	23	25
Wing	Range	151–163	152–160	148–161	148–163	142–158	144–160	142–160	144–153	147–162	141–157
	Mean with standard error	157.4±.48	156.2±.65	155.1±.59	156.3±.36	149.9±.73	153.2±.54	151.34±.64	150.3±.78	154.8±.98	148.8±.88
	Standard deviation	3.2	2.45	3.5	3.45	4.0	2.83	4.82	2.58	4.7	4.4
Tail	Range	75–90	79–89	75–90	75–90	71–86	74–85	71–86	75–85	69–86	72–88
	Mean with standard error	84.4±.38	83.8±.86	83.1±.50	83.8±.31	79.4±.51	79.9±.47	79.5±.42	78.9±.89	74.4±.80	79.4±.66
	Standard deviation	2.58	3.11	2.99	3.01	2.74	2.61	3.18	2.96	4.23	3.10
Bill	Range	15–17	15–17	14.5–16.5	14.5–17	14.5–16	14–16.5	14–16.5	14.5–15.5	13.5–15.5	13–15
	Mean with standard error	15.9±.06	15.4±.15	15.3±.07	15.6±.06	14.9±.07	15.1±.09	15.09±.06	14.9±.09	14.0±.11	14.1±.13
	Standard deviation	.44	.56	.46	.53	.40	.48	.48	.29	.56	.61

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No. 8.—*Airplane Observations of Homing Pigeons*

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INTRODUCTION

The homing of domestic pigeons and the migrations of wild birds are often considered as comparable cases of natural navigation. In both types of long distance flight it is difficult to discover adequate guiding cues that lie within the sensitivity range of the birds' sense organs. Hence in both cases the theories advanced to explain the birds' orientation have been diverse, speculative, and sometimes fantastic. In other respects the two types of natural navigation are different. Pigeons must be trained; but wild birds train themselves or perhaps learn from their fellows. At least on its first migration a wild bird seeks a goal it has never visited; whereas the pigeon is always returning to a familiar home. Long annual migrations of wild species are linked to seasonal patterns of climate, activity, and reproduction, while pigeons may home at any season and without any immediate incentive other than the attraction of the home loft itself.

The accumulated evidence concerning the sensory basis of navigation in homing pigeons has been reviewed by Claparède (1903), Watson and Lashley (1915), Heinroth and Heinroth (1941) and Griffin (1944). This evidence stems from the most diverse sources, ranging from the anecdotes of pigeon racing enthusiasts to the most painstaking type of scientific experiments, such as those of Sigmund Exner (1905). Fruitful interpretation of even the more carefully controlled experiments is hindered, however, by the rarity of incontestable records of straight flight towards the home loft over territory completely unfamiliar to the pigeons. In most cases the time required for return from distant release points in unfamiliar territory was great enough to leave considerable room for doubt whether, on the one hand, the homing flight had been essentially direct but included stops for rest or other purposes, or on the other hand, might have involved extensive wandering or exploration in search of familiar territory.

Direct observation from airplanes has recently thrown some light on the actual routes which wild birds fly in finding their way home to their nests after being artificially transported to a distance. Herring gulls and gannets were observed to make exploratory flights in many directions, flights which covered a wide area surrounding the release point and which probably brought the birds, in time, within sight of familiar landmarks (Griffin, 1943; and Griffin and Hock, 1949). Homing by exploration was suggested for pigeons many years ago (Hodge, 1894; Claparède, 1903; Rabaud, 1928; Rivière, 1929; and Gundlach, 1932). It therefore seemed desirable to apply to pigeons the same technique of airplane observation which had been developed for use with wild birds.

Fifteen observation flights over distances up to 100 miles disclosed several cases in which the birds appeared to be relying upon exploration or topographic landmarks. But in other instances there was a definite tendency for the pigeons to head in the approximate direction of home, even when flying over what was almost certainly unfamiliar territory. Despite the fact that no final conclusions can be drawn from the results of these observations, the homing behavior of these pigeons is of interest in view of the scarcity of precise, adequately controlled descriptions of the actual routes between release point and home loft.

Grateful acknowledgement is made to the Office of Naval Research for financial support which permitted the completion of this series of airplane observations in 1947, through a research contract with Cornell University.

METHODS

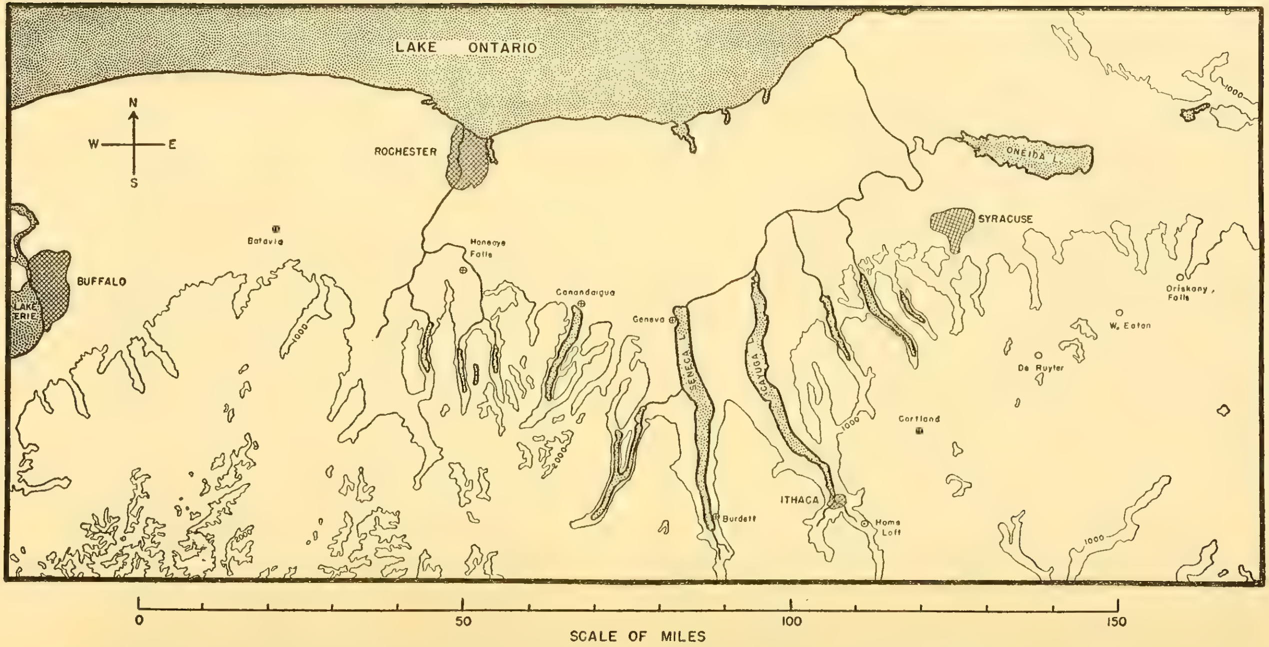
The pigeons used in these investigations were the progeny of birds whose previous owners reported rapid homing flights of 100 to 500 miles. The majority were of dark colors, but a number of pure white pigeons were included in the flock since they are much more easily visible from the air. In all of the airplane observations reported below one or more white birds were in the group that was followed. White pigeons are seldom used by pigeon racers, chiefly because they seem to be more susceptible to attacks by hawks. Hence there has not been any intensive selection to develop racing strains of white pigeons, and certainly my white birds showed heavier losses than those of the darker colors.

Of the pigeons mentioned below, Nos. 4–17 were hatched and raised in a loft five miles S.W. of Ithaca, N. Y., while Nos. 34–49 (all white birds) were purchased at an early age and trained with other young pigeons. In all cases the birds were carried to distances which are customary in races involving pigeons of their age; thus Experiment I employed birds of four and five months in flights of 25 miles or less, while for Experiment II, which included flights from as far as 100 miles, the birds were at least one year old.

The loft was of conventional construction with a one-way entrance or "trap" that allowed the pigeons to enter a small cage where they remained until inspected and allowed into the loft proper. After each release, including all training flights, the loft was visited often enough to ascertain which birds had flown a reasonably straight course home, and which might have remained out long enough for extensive wandering. The daily exercise and training flights at short distances were restricted to the late afternoon, usually to the last two hours of daylight. This set limits to the amount of territory with which the birds could become familiar; and throughout the experiments an attempt was made to minimize the time available for uncontrolled wandering. This effort was not entirely successful, for several birds remained away overnight on one or more occasions during their training; and the maximum time away from the loft is given below for each bird observed from the air.

In airplane observations the same general methods were used as with wild birds (see Griffin, 1943; and Griffin and Hock, 1949); an altitude of 800 to 1000 feet above the ground was maintained and the pigeons scarcely ever flew at altitudes greater than 100 feet. The presence of the airplane at this altitude did not appear to affect the birds' behavior in any way. A single white pigeon, or a group containing a white bird, could be followed without undue difficulty, but the dark colored birds could not be traced successfully except in larger flocks than were available for these experiments. During the preliminary training flights from distances of one to ten miles the birds were accustomed to the presence of aircraft by several releases near airports and by two short flights in which they were observed from the air. Two- or three-place high-wing monoplanes of 65 to 100 horsepower were used for all observations.

The summer and autumn of 1946 were devoted largely to the preliminary training of pigeons for the observations made with yearling birds in 1947. The increase in distance was very gradual so that up to 20 miles the birds were never released more than two or three miles beyond familiar landmarks. In the fall of 1946 four white birds were utilized for Experiment I, designed to study the orientation of young pigeons in unfamiliar territory. In that experiment, and in the releases


LAKE ONTARIO
N
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E
S
ROCHESTER
ONEIDA L.
SYRACUSE
1000
Batavia
Honeoye Falls
BUFFALO
LAKE ERIE
Canandaigua
Geneva
SENECA L.
CAYUGA
Oriskany, Falls
W. Eaton
De Ruyter
Cortland
ITHACA
Burdett
Home Loft
0
50
100
150
SCALE OF MILES

Fig. 1. General area over which the pigeons made their homing flights.

at greater distances during 1947, most of the longer flights were observed from the air, so that at the time of each successive release something would be known of the birds' previous experience and familiar territory.

The general topography of the area in which all of these flights took place is shown in Figure 1; and the details of individual flights are described below, and illustrated in the maps of Figures 2 to 6.

EXPERIMENT I

1. *General plan and preliminary training.*

This experiment employed four white pigeons four to five months old (Nos. 6, 8, 9, and 21); they were first observed during a flight over familiar ground and were then followed from the air as they sought to find their way home from unknown territory. They were given preliminary training by numerous releases in an area extending ten miles northwest, seven miles west, two miles southwest, three miles south, two miles southeast, three miles east, and 21 miles northeast. After one of the later training releases in familiar territory northeast of home, they were followed by airplane. They were next carried 24 miles WNW and released in quite unfamiliar territory where the topography resembled that of a familiar area bordering the south end of Cayuga Lake.

Most of the preliminary training flights were made in the company of other pigeons; but each bird was also released alone on several occasions, so that all had had experience in returning from familiar territory without any possibility of guidance by others of the flock. Nos. 6, 8, and 9 had each completed a total of 39 training flights while No. 21 had made 25. The more distant of these release points employed in the preliminary training are shown in Figure 2 by circles with an enclosed cross. The releases were timed so that the birds never had more than two to three hours of daylight in excess of time required for a direct flight home. If they were back at the loft by nightfall or early the next morning, it was very unlikely that they had wandered to points far removed from the area included in Figure 2.

Two birds, Nos. 6 and 9, never remained away from the loft overnight during this training period, but the other two did have occasional lapses. Number 8 remained out overnight after one release at 7 miles, and after another at 10 miles; after a second release at 7 miles it remained out for two days. Number 21 stayed out overnight following two releases at 7 and 11 miles, and it remained away from the loft for 36 hours after a release at 8 miles. It was thus possible that these two birds had wandered extensively, and had a large area of familiar territory, although the experience of pigeon racers suggests that such lapses at a relatively early stage in a pigeon's training are caused by preoccupation with rest or feeding rather than extensive wandering. Furthermore, when the group was later released in unfamiliar territory, the bird that exhibited by far the best homing performance was No. 9, which had never remained out overnight, rather than No. 8 or No. 21.

2. *Airplane observation of a flight over familiar territory.*

After the preliminary training outlined above, the four white pigeons were released 11:45 A.M., October 21, 1946, at the Cortland airport and followed during their entire flight to the home loft. As can be seen from Figures 1 and 2, the Cortland airport is 17 miles northeast of the loft. The birds had been released there once before on October 16, and in addition they had been released October 20 at Homer, four miles farther from the loft, so that they had flown over Cortland area on two previous occasions.

After a 10 minute period of circling in the immediate vicinity of the release point (the usual behavior which preceded homing flights by these pigeons), the four birds were joined by a larger flock of local pigeons. Together with these birds they circled over an area southwest of the airport, but finally separated from the local birds and began, about 15 minutes after release, to move along the route shown in Figure 2. During the first five miles they circled continuously, but the trend of their circling was always westward, i.e., slightly to the north of the true course home. When about five miles from the release point their manner of flight changed rather abruptly to straight flight along the course shown. Thereafter their progress was steady with very few sudden turns until they reached their home loft 70 minutes after release. Disregarding preliminary circling, the actual flight path was about 21 miles in length, while the airline distance from release point to home was 17 miles.

3. *Airplane observations in unfamiliar territory with confusing topography.*

The Cortland flight showed that the birds, while neither as fast nor as sure of themselves as highly trained racing pigeons, nevertheless flew an essentially straight course when released in familiar territory.

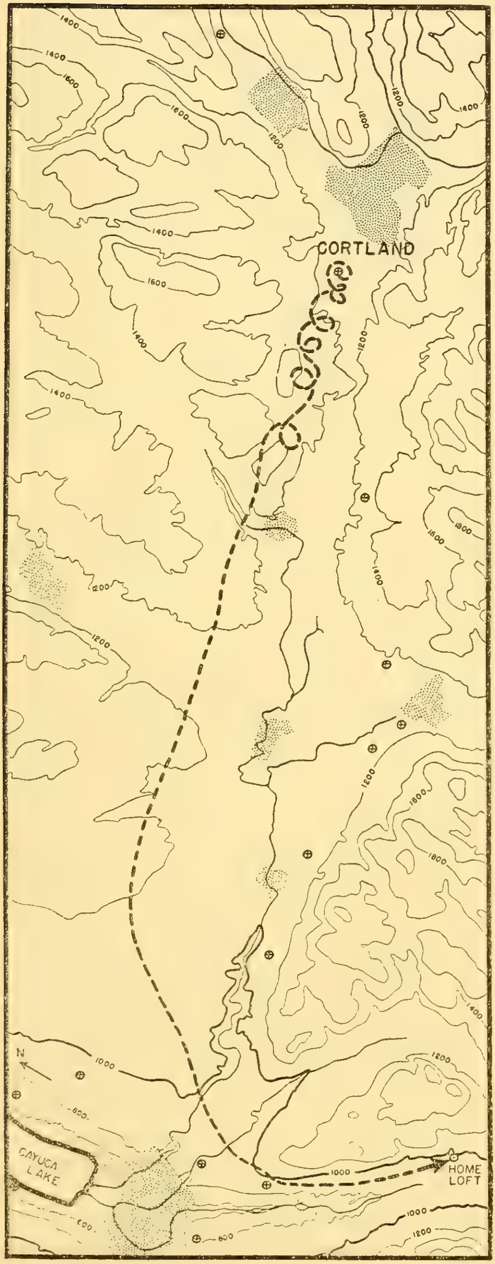
CORTLAND
1400
1600
1200
1800
1000
800
N
CAYUGA LAKE
HOME LOFT
CITIES or TOWNS
0
1
2
3
4
5
MILES

Fig. 2. Route flown by four pigeons over familiar territory in Experiment I. The actual flight path during the first three miles contained even more loops and turns than are indicated. Previous release points are shown on the map by circles with an enclosed cross; note that while the birds flew down the same valley as that traversed during the transportation to earlier release points they did not fly directly past these points.

The next step was to repeat the observation from roughly the same distance into unknown territory. The geography of the Finger Lakes area permitted the addition of a geographical factor which offered some chance of revealing how much the birds depended upon topography. The home loft lay six miles southeast of the southern end of Cayuga Lake, in one of the two well-defined valleys leading south from this end of the lake. Such topographic features, in addition to the presence of the small city of Ithaca at the end of the lake, should be useful for visual orientation of birds released near Ithaca, as these birds had often been. The Finger Lakes are all similar in geological origin and general shape (see Fig. 1); Cayuga and Seneca Lakes have especially similar topography at their southern ends. In both cases there are (1) flat alluvial plains extending one to three miles immediately south of the end of the lake, (2) steep hillsides on both sides of the lake along the southern half of its length, and (3) hills directly south, beyond the alluvial plain, which are divided by two valleys, each containing a small creek. Furthermore, there are cities on both alluvial plains, although these are quite different in appearance. It thus seemed possible that pigeons familiar with the south end of Cayuga Lake might be misled by this similarity when released at the south end of Seneca Lake.

The first release point in unfamiliar territory was therefore placed near Burdett at point A of Figure 3, 23.6 miles WNW from the home loft. This point was analogous to a release point on the eastern shore of Cayuga Lake where the four birds had been released several times during their preliminary training (see Fig. 2). If the pigeons relied upon topography for their orientation, they might be expected to fly south from release point A into the valley leading southeast from Seneca Lake, whereas a true course towards their home would take them ESE. The difference between these two hypothetical courses was about 85 degrees.

The actual release at point A was made at 11:05 A.M., October 27, 1946. In the interval since the flight from Cortland the pigeons had been given two short exercise flights by releases five miles west and 12 miles NNW from the loft. On the 27th they circled for about 15 minutes within a mile of release point A, and then turned abruptly south. The flight south was continued for about 2¼ miles, and at this distance from release point A the birds turned to the east as shown in Figure 2. By this time they were in a region where the topography was clearly different from that of their familiar territory near Ithaca.

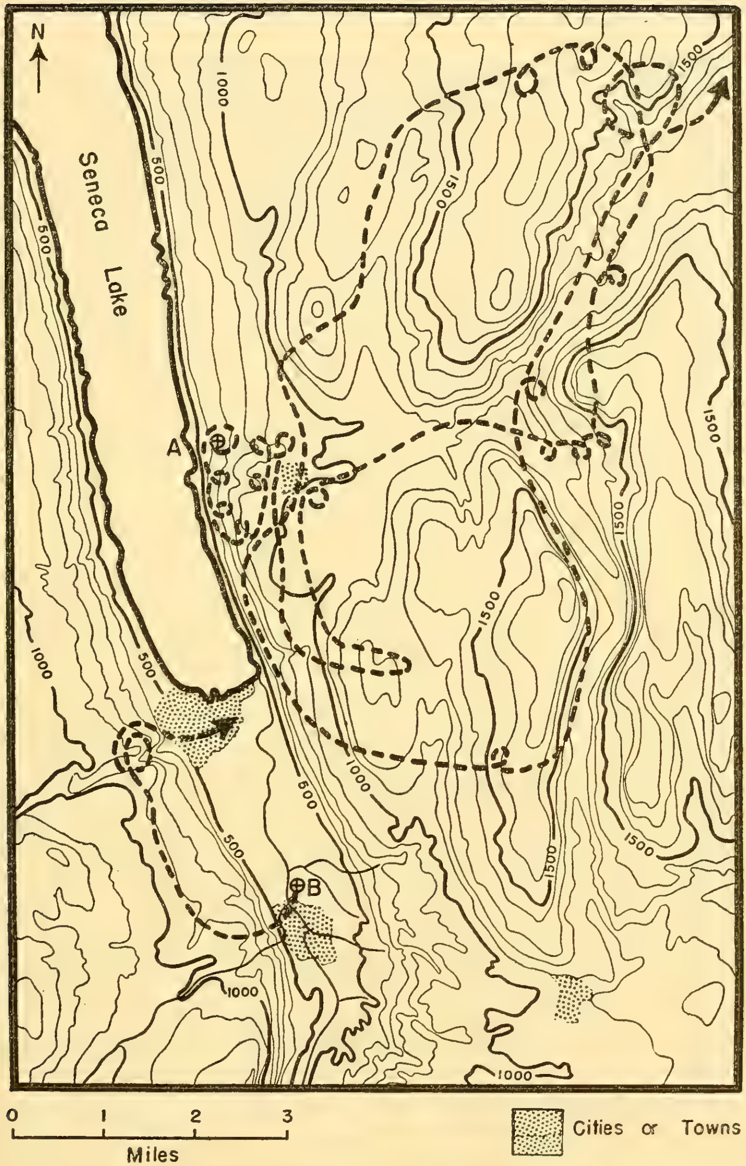
N
Seneca Lake
A
B
500
1000
1500
0 1 2 3
Miles
Cities or Towns

Fig. 3. Route flown over unfamiliar territory by the same four pigeons (as in Fig. 2). Point *A* was 23.6 miles WNW from the home loft, at a point near the shore of Seneca Lake that was analogous to a previous release point near Cayuga Lake. Note that on two occasions the birds flew *south* when departing from the vicinity of the release point; this is the direction they would be expected to take if they were misled by the topographical similarity between the two lakes.

After their turn to the east the pigeons returned to Burdett, circled over the village, turned east through a valley and continued along the course shown in Figure 3, which led them back to the vicinity of the release point. Again the birds flew south from Burdett, but this time flew three miles before turning east and then north once more. At one hour and forty minutes low fuel supply forced us to discontinue the observation at a time when the birds were heading northeast. Throughout the period of observation the four birds stayed together, and they flew 35 miles altogether, aside from local circling. Yet at the end of the observation they were only seven miles from the release point, heading 77° north of the correct course towards the home loft. Only one of the four, No. 9, returned to the loft at all, and it required four hours and forty-five minutes for the flight. This should be contrasted with one hour and ten minutes required for the return of the entire group from Cortland over familiar territory.

Pigeon No. 9 was again released at the south end of Seneca Lake (at point B of Fig. 3) at 11:08 A.M., November 9th. The airplane observation of No. 9 on this date was unfortunately terminated after a few minutes, when the pigeon was lost to view against a cluster of white houses in the city of Watkins Glen. But it was back at its loft when I first returned to look for it 1½ hours later.

The results of Experiment I show clearly that these four young white pigeons were unable to determine the correct direction of their home when released at 23.6 miles in what was evidently unfamiliar territory. The nearest of their previous release points to Seneca Lake was only seven miles from home, so that they had been suddenly carried across 16 miles of hilly territory over which they had no occasion to fly during the preliminary training. The general pattern of their flight suggested that they lacked any clear orientation and conformed to expectations of theories based upon recognition of visual landmarks.

As in most homing flights of pigeons there was a clear separation between the initial period of circling or undirected short flights within a mile or so of the release point, on the one hand, and the rather sudden beginning of a definitely "cross-country" flight which continued in approximately the same direction for a matter of miles. In this case the initial period lasted 15 minutes, and the shift to cross-country flight was abrupt and recognizable at the time it occurred. As noted above, both cross-country flights away from the release point were directed south, just as one would expect if the birds were guided by the topographical similarity between the southern ends of the Cayuga and Seneca Lake basins. It is not surprising that this topographical delusion failed to persist all the way to a point analogous to the location of the home loft southeast of Cayuga Lake. When the birds had flown south for two to three miles the different appearances of the two lake basins should have become quite obvious; for this flight was largely over open fields, whereas the analogous flight path south from a corresponding point on the shore of Cayuga Lake would have taken the birds over a residential section of Ithaca and over the Cornell campus.

Another not uncommon behavior pattern of inexperienced or disoriented pigeons is to fly for several miles in a closed circuit that returns to the release point after 20 to 30 minutes. This type of flight has been described to me by pigeon racers and, as shown in Figure 3, it occurred after this release of pigeons at point A near Seneca Lake.

EXPERIMENT II

1. *General plan, and previous experience of the birds.*

In the spring of 1947 a flock of 13 experienced pigeons was available, all approximately one year old; seven were white (Nos. 9, 34, 35, 36, 45, 48, and 49), and six were dark colored (Nos. 4, 12, 14, 15, 16, and 17). The previous experience of No. 9 has been described under Experiment I; after the second release near Seneca Lake it had made only short exercise flights and was never out overnight. Nos. 34–49 had been purchased in the fall of 1946 as young birds never flown from their natal lofts; but all of the dark colored birds had been raised at my loft in 1946 and had acquired considerable flying experience. In the course of 26 preliminary training flights from March 23 to May 22, 1947, this flock was brought into good flying condition by releases at several points within an area extending three to five miles east, south and southwest from the loft, 21 miles west, 13 miles northwest, and 5 miles north. In addition Nos. 4, 12, 14, and 15 had made three longer flights during 1946 from release points to the northeast of the loft, all of which are shown in Figure 1. On September 22, 1946, these birds were released at DeRuyter, N. Y., 42 miles northeast, at 3:45 P.M.; all were back at the loft by 6:30 P.M. On September 26 they were released at West Eaton, N. Y., 52 miles northeast, at 4:15 P.M.; three were again back by nightfall and the fourth, No. 12, was home by 7:30 A.M. the following morning. The longest of these flights was made October 4, when three of the birds, Nos. 4, 14, and 15 were released at 1:00 P.M. near Oriskany Falls, 65 miles northeast of their home loft. Nos. 14 and 15 reached the home loft at 4:26 P.M., but No. 4 did not return until sometime between 5 P.M. October 5 and 9:00 A.M. October 6. Thus all flights except the return of No. 4 from Oriskany Falls occurred with sufficient speed to assure that no extensive wandering from the direct course home could have taken place.

In Table 1, I have summarized the previous experience of the 13 pigeons used for Experiment II, together with the most serious cases where their return was slow enough to allow for possible wandering into the area of later releases. In each case the instance of slow homing listed was the worst one in the bird's record, and none of its other lapses could have significantly increased the probability that the later release points of Experiment II had been visited. In Table 1, the homing times refer to the time when the bird was actually seen at the loft; in some cases a day or two elapsed between complete checks, so that some of these pigeons probably returned considerably sooner than indicated in the table.

The general plan of Experiment II was to release the flock at progressively greater distances northwest from Ithaca, following the birds from the air after each release in unfamiliar territory. Because of occasional slow returns before the final releases at 55 miles or more, it is not possible to establish with complete certainty that any individual release was made in what was unfamiliar territory for every bird in the flock. But the probability that *all* of the more distant release points had been visited previously appears extremely small, and the results as a whole cannot reasonably be explained as orientation based exclusively upon familiar landmarks and exploration. The routes flown by various birds are presented in Figures 4, 5, and 6, and the pertinent observations on individual behavior are contained in a condensed summary of each observation. It was unfortunately not possible to provide a continuous watch for returning birds at the loft; but unless stated otherwise, all of the birds returned soon enough after release to establish the fact that they had flown home without extensive detours.

2. *Description of individual flights.*

Covert, 19 miles northwest; birds released 12:35 P.M., May 24, sky almost fully overcast, warm, hazy, visibility five miles, calm. The flock circled within half a mile for 10 minutes, then in larger circles tending more to the south

TABLE 1. Previous history of pigeons used in Experiment II, and their homing performance during the experiment. An asterisk, *, indicates a sufficiently early return to show nearly straight flight home; in all other cases the maximum homing time is given. Parentheses, ( ), indicate that the bird was not flown.

Pigeon number	4	12	14	15	16	17	9	34	35	36	45	48	49
Color	blue bar	blue check	blue bar	blue bar	blue bar	red	white	white	white	white	white	white	white
Longest flight in 1946	65 m. NE.	52 m. NE.	65 m. NE.	65 m. NE.	( )	22 m. NE.	24 m. WNW.	( )	( )	( )	( )	( )	( )
Slowest previous homing flight	41 hrs. at 65 m. NE. (1946)	48 hrs. at 21 m. NE. (1947)	always a good homer	over-night at 11 m. in 1946	5 days (first flight, 1946)	5 days (first flight, 1946)	always a good homer	always a good homer	overnight at 15 m.	48 hrs. at 21 m. WSW.	48 hrs. at 21 m. WSW.	several days at 4 m.	4 days at 21 m. WSW.
Covert May 24, 12:35 P.M.	*	*	*	*	*	*	*	*	*	*	*	*	( )
Interlaken May 26, 3:07 P.M.	*	24 hrs.	*	*	2 days	*	*	*	2 days	24 hrs.	*	24 hrs.	( )
Covert May 31, 3:25 P.M.	*	*	*	*	*	*	*	*	( )	( )	*	*	*
Interlaken June 1, 2:30 P.M.	*	*	*	*	*	*	*	*	*	*	*	*	*
Scott's Corner June 10, 3:27 P.M.	overnight	*	overnight	*	overnight	*	*	overnight	overnight	overnight	*	overnight	*
Willard June 13, 1:23 P.M.	*	*	*	*	*	*	*	Newark June 16	*	*	lost	*	*
W. Fayette July 15, 11:25 A.M.	2 days	*	Richland July 21	*	*	*	*	lost	2 days	*		lost on exercise flight	7 days
Geneva July 23, 3:01 P.M.	*	*		*	4 days	*	*		*	*			*
Canandaigua July 25, 2:42 P.M.	*	*		*	( )	*	*		lost	*			*
Interlaken Sept. 23, 3:35 P.M.	*	*		*	1–4 days	*	22 hrs.			22 hrs.			1–4 days
Ovid Sept. 27, 9:50 A.M.	*	*		*	*	*	*			*			*
Geneva Oct. 2, 2:53 P.M.	*	*		*	*	*	*			*			*
Canandaigua Oct. 7, 2:15 & 4:15 P.M.	*	*		*	*	*	*			Webster Oct. 11			lost
Honeoye Falls Oct. 12, 11:02 A.M.	20–24 hrs.	lost		lost	killed near Trumansburg	lost	20–24 hrs.						
Batavia Oct. 21, 1:40 P.M.	lost						lost						

and east than north and west. Four or five times they returned to the release point. At 20 to 25 minutes they came within sight of Cayuga Lake and suddenly turned towards its shore (see Fig. 4). On reaching the lake they flew south along the shore until at four miles north of Ithaca they crossed the lake and continued south along the east shore and thence directly home to reach the loft 55 minutes after release.

Interlaken, 22 miles northwest; birds released 3:07 P.M., May 26; clear, visibility unlimited, polar continental air mass, wind southwest, moderate, sharp updrafts, cumulus clouds forming by the end of observation. The birds circled within 0.3 mile for 13 minutes, then flew east or ESE to reach Cayuga Lake (which was visible from the release point) at about the same point as on May 24. They then flew south along the west shore of the lake as shown in Figure 3 and were lost to view over Ithaca. Numbers 12, 36, and 48 were out overnight, and Nos. 16 and 35 did not return until two days after release.

Covert, 19 miles northwest; birds released 3:25 P.M., May 31. They were not followed by air, but were observed from the ground to fly off to the west, return ten minutes later to the release point, and then head south.

Interlaken, 22 miles northwest; birds released 2:30 P.M., June 1; solid overcast, visibility eight to ten miles, gentle SSE wind, light rain just before and after flight. The birds circled 15 minutes, mostly to the south, then headed east. Two miles from release point the flock split; one group continued southeast and another, which I followed because it contained three white birds, continued SSE along the main highway, thus passing close to all of the previous release points (see Fig. 4). In fact, they seemed to seek out these spots, flying within 200 to 300 yards of each previous release point and circling over the one at Trumansburg, although at other times they deviated a quarter to a half mile from the highway.

Scott's Corner, 25 miles northwest; birds released 3:27 P.M., June 10; clear, warm, slight haze, visibility eight miles, a few cumulus clouds forming, light south wind. The birds circled near the release point for 17 minutes, flying more often to the south and east than in other directions. They then flew ESE with some veering, reached Cayuga Lake near Shelldrake Point, and turned south along the lake shore after first flying 200 yards out over the water (see Fig. 4). Fifty-eight minutes after release the flock under observation contained five white and three dark birds, and these eight landed on the shore of the lake near Jacksonville so that they could not be followed farther from the air. Numbers 4, 14, 16, 34, 35, 36, and 48 remained out overnight; that is, three dark and four white birds. This is only one bird less than the number seen to land, so that it seems likely that other activities than wide wandering caused this slow homing.

Up to June 10 the birds were given every opportunity to learn the topography and landmarks. They were carried to the release points in a cage attached to the roof of an automobile and not only was each release point within sight of the previous one from an altitude of 100 to 200 feet, but all were within two

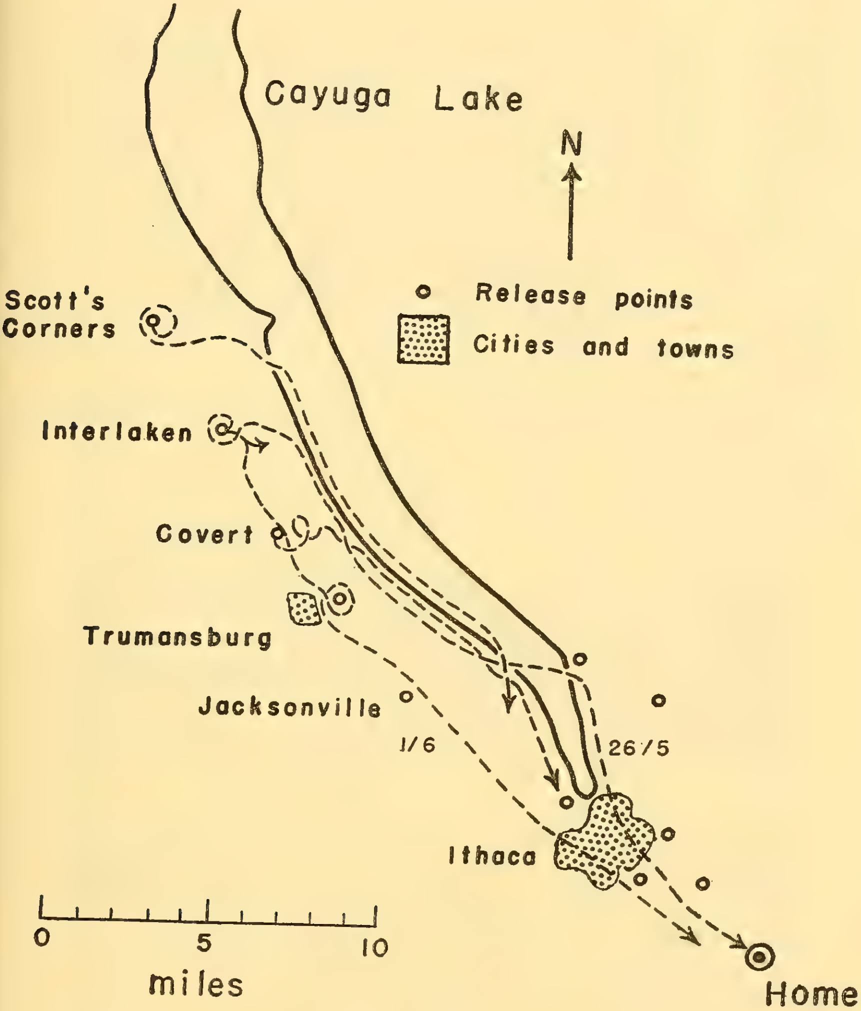
Cayuga Lake
N
Release points
Cities and towns
Scott's Corners
Interlaken
Covert
Trumansburg
Jacksonville
1/6
26/5
Ithaca
0
5
10
miles
Home

Fig. 4. Routes flown by pigeons during the early stages of Experiment II; all these release points were within a mile or two of familiar territory. Note that after the release at Interlaken on June 1 the birds that were being followed flew directly over several of the previous release points.

miles of Cayuga Lake. The birds returned in all observed cases by following the shore line of the lake, or in one case by flying along the highway leading past all of the previous release points. After June 10, however, the birds were carried in closed boxes inside the automobile or airplane and were taken to release points separated by greater distances. Table 1 shows that the losses increased sharply when these changes were made. Clearly the releases after June 10 provided a more strenuous test of the pigeons' homing ability.

Willard, 32 miles northwest; birds released 1:23 P.M., June 13, partly overcast, moderate south wind, visibility about 15 miles, moderately bumpy air with high stratus and stratocumulus clouds. This release provided an opportunity to test the influence of topography, for the birds had previously been released close to Cayuga Lake (Fig. 4) and on reaching it had only to turn right and follow the shoreline in order to reach Ithaca. At Willard, however, they were released about 1½ miles from Seneca Lake as shown in Figure 5. If they relied upon simple topographical orientation one would expect them to circle, notice Seneca Lake, fly to it, turn right along its shore, and head north — almost directly away from home. The birds circled for only about five minutes, then flew southwest and reached the shore of Seneca Lake at ten minutes. So far they had behaved roughly as would be expected on the basis of the topography. On reaching the lake, however, the flock turned south, flew inland about one-half mile to a railroad track along which they continued southward. About one mile south of the village of Willard the flock split, four white birds continuing south, and others turning back to the north. There were at least two white birds in the latter group, and almost certainly they were Nos. 34 and 45 which failed to find their way home. One of these, No. 34, was picked up at Newark, N. Y., on June 16, and later returned to me. Newark lies 28 miles NNW from Willard (see Fig. 5) and it seems quite possible that these two white birds broke away from the flock because they were indeed misled by the topographic resemblance to previous release points near Cayuga Lake.

The group which continued south, containing four white birds, flew a surprisingly straight course towards home, as shown in Figure 5, despite the fact that this course led them over many miles of territory never previously visited when under observation. But some of these pigeons might have visited the Willard area during one of the longer periods away from home after an earlier release (for example, No. 35 had been out for two days after the release at Scotts' Corner, and Nos. 12, 16, 21, and 45 may have been out as long as 48 hours after a release 21 miles WSW of the loft).

After reaching the city of Ithaca the group made a detour across the valley extending southwest from the end of the lake, instead of flying southeast to their home loft. This detour inside of very familiar territory is difficult to understand; it should be compared with another detour within familiar territory that occurred on July 25 after the first release at Canandaigua.

West Fayette, 38 miles northwest; birds released 11:25 A.M., June 15; high

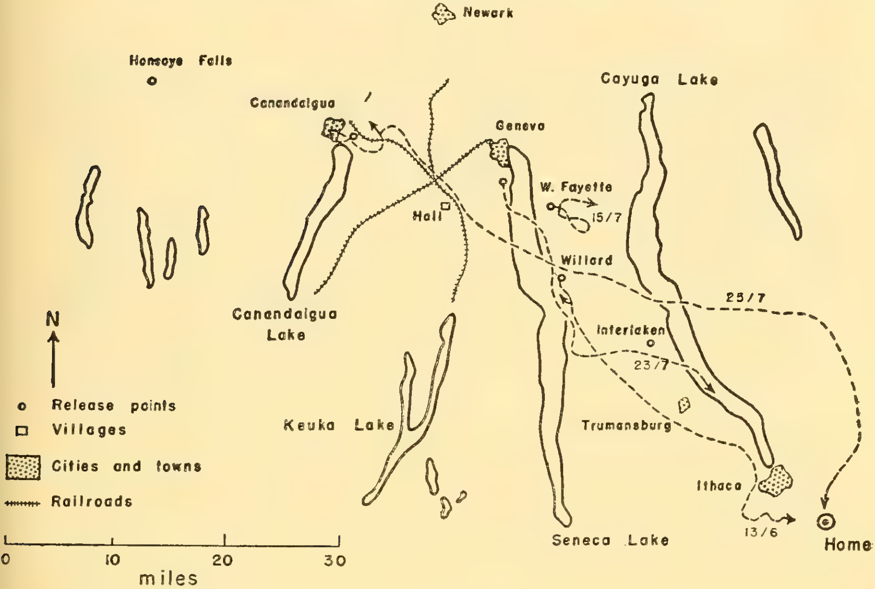
Newark
Honeoye Falls
Canandaigua
Geneva
Cayuga Lake
W. Fayette
15/7
Hall
Willard
25/7
Canandaigua Lake
Interlaken
23/7
N
Release points
Villages
Cities and towns
Railroads
Keuka Lake
Trumansburg
Ithaca
13/6
Home
Seneca Lake
0
10
20
30
miles

Fig. 5. Routes flown in Experiment II after releases at 32 to 55 miles from home, in what was probably unfamiliar territory. Note the generally correct direction taken in most instances. The observed flight path of No. 34 after its release at Willard is indicated by the small arrow branching away from the path taken by the main flock; this bird was recovered at Newark, and may have been misled by the lake topography. Note also the case of an apparent "overshoot" across familiar territory after the release at Canandaigua on July 25.

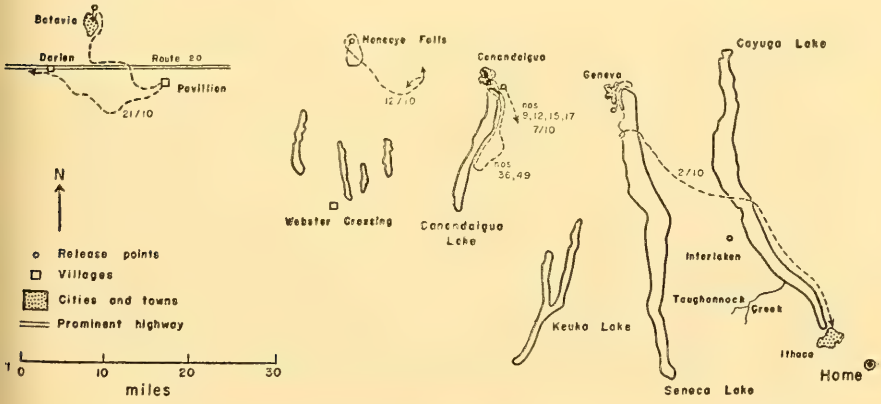
Batavia
Darien
Route 20
Pavilion
21/10
Honeoye Falls
12/10
Canandaigua
nos
9,12,15,17
7/10
nos
36,49
Geneva
Cayuga Lake
2/10
N
Webster Crossing
Canandaigua Lake
Interlaken
Release points
Villages
Cities and towns
Prominent highway
Taughannock
Creek
Keuka Lake
Ithaca
Home
0
10
20
30
miles
Seneca Lake

Fig. 6. Routes flown after the second releases at Geneva and Canandaigua, and after the final releases at Honeoye Falls and Batavia in what was almost certainly unfamiliar territory. Note the nearly correct initial flight direction in all cases.

solid overcast with lower cumulus clouds at 2500 feet, scattered showers, hazy, visibility 4 to 5 miles, moderate SSE wind. These were the most adverse weather conditions, and also the poorest visibility, of any release involving airplane observation. The birds circled for 20 minutes, then started southeast as shown in Figure 5, but after 1½ minutes turned east and flew to within three miles of Cayuga Lake (which, however, was not visible). There they turned south, and then back to the west, next northwest, and finally returned to the release point 35 minutes after they had been set free. They next flew ENE and east and were finally lost to view 55 minutes after release. Pigeon No. 34 was released separately from the other birds in order to see whether its wanderings between Willard and Newark had had any effect. It was not followed from the air, but it headed west from the release point and never returned. The main group also did poorly. The first birds returned after six hours, and No. 14, which had previously appeared to be one of the best fliers, was found six days after release at Richland, N. Y. — 68 miles northeast of the release point. Numbers 4 and 35 were out for two days and No. 49 was not back until a week after release. Here was striking confirmation of the pigeon racers' experience that weather involving very poor visibility has an adverse effect on pigeons' homing performance.

Geneva, 43 miles northwest; birds released 3:01 P.M., July 23; almost solid overcast at 5000 to 6000 feet and half coverage of cumulus clouds at about 3000 feet, strong updrafts, wind generally west. The birds circled near the release point for 17 minutes, with two false starts to the south along the shore of Seneca Lake; after each of these southward flights they returned to the release point. They next flew south for two miles, turned sharply east across the lake, and turned south again along its eastern shore as shown in Figure 5. This portion of the flight crossed terrain over which they had flown on June 13, but now they continued south along the lake shore about two miles farther than on the 13th. There the flock split, and we followed two white birds which flew straight east along a road which led them into Interlaken. Next they flew southeast to Cayuga Lake and continued home along its west shore just as they had done on so many previous flights. Number 16 remained out for 4 days after this release.

Canandaigua, 55 miles northwest; birds released 2:42 P.M., July 25; four-tenths coverage with cumulus clouds, visibility eight to ten miles, modified polar continental air mass, warm, light westerly winds with surprisingly smooth air. This release represented the longest step yet taken into presumably unfamiliar territory. The birds circled the release point for 23 minutes, including a flight one mile to the south; but they returned frequently to the release point. They then flew west over the city of Canadaigua, returned once again to the release point, and next headed ESE along the route shown in Figure 5. When the main flock made a turn to the north one white bird separated from the rest by turning farther and heading northwest. The main group flew along a railroad for some distance as shown in Figure 5, and after reaching Seneca Lake followed roughly the same route as that flown from Geneva to the west shore of Cayuga Lake on July 23. Here, however, they surprised us by continuing directly east across Cayuga Lake and holding to the same direction for 15 miles more. As shown in Figure 5, they eventually turned south and reached territory which must have been familiar from flights made in 1946. It is even possible that the whole area ten to fifteen miles east of Cayuga Lake had been visited by one of the birds either in 1946 when returning from releases up to 65 miles northeast, or during the long period required to return from the West Fayette releases on July 15. But why these birds flew so far east of Cayuga Lake is difficult to explain, for they were already at the shoreline along which they had flown home on previous occasions. The whole performance is reminiscent of pigeon racers' description of an "overshoot". This is reputed to be a flight in which pigeons continue flying in the same direction, passing their own loft and landing at some other loft in the same city which lies farther from the release point than their own home. Number 35 was lost on this flight, and it may well have been the single white bird that broke away to the northwest shortly after the flock left the vicinity of Canandaigua.

After this 12-mile step into presumably unfamiliar territory, the birds took essentially the correct direction, except for short flights near the release point, just as they had done at Willard. It is far less likely that they could have found familiar landmarks near Canandaigua, however, for no exploratory flights west of Geneva had been observed. Nevertheless, there had been opportunity for wandering into the Canandaigua area after the release at West Fayette, when Nos. 4 and 35 were out for two days and No. 49 may have been out for as long as seven days, and also after the release at Geneva, when No. 16 may have been out as long as four days.

During August it was not possible to make further observations of these pigeons. They were given two short practice flights from Interlaken (3:35 P.M., September 23) and Ovid (9:50 A.M., September 27); on the first flight, No. 9 stayed out overnight and Nos. 16 and 49 remained away from the loft for four days. Evidently their homing ability, or more likely their physical stamina for long flights, had been impaired by two months with no activity except exercise flights in the immediate vicinity of the loft.

Geneva, 43 miles northwest; birds released 2:53 P.M., October 2; high broken altocumulus clouds and occasional sunshine, visibility 10 to 12 miles with patches of haze, wind northwest 10–12 mph at the outset but dropping to five mph at the end of the observations. The birds circled for twenty minutes at the release point, making during that period two flights of one half mile to the south and back to the release point. They next flew north over the city of Geneva, returned once again to the release point, and finally headed south along the route shown in Figure 6. During the ensuing southward flight along the lake shore they twice flew out over the water for 200 to 300 yards and then returned to the land. It was tempting to infer that two dark birds which in each case flew farther from land than the rest were attempting to lead the flock across the lake. The flock did turn sharply to the east and crossed Seneca Lake only when it arrived at the point where the birds had reached the lake on their flight from Canandaigua on July 25. The remainder of this flight followed routes flown on previous occasions.

Canandaigua, 55 miles northwest; birds released October 7; clear, hot, visibility 15 miles with slight haze in patches, gentle southwest winds. The flock was divided into two groups; the first group to be released (Nos. 4, 16, 36, and 49) were carried from Geneva to Canandaigua at the window of the airplane in an attempt to "show" them the terrain. After being set free at 2:15 P.M. these four birds interrupted their initial circling near the release point by a sojourn on the roof of a barn and silo in the company of local pigeons; but at 30 minutes after release the four birds circled several times over the city of Canandaigua and the north end of Canandaigua Lake. At this time the two white birds separated from the others and were followed south along the route shown in Figure 6. After another return to the release point at 68 minutes after release these two white birds spent another 20 minutes over the city of Canandaigua before being lost. Neither returned to the loft; but one, No. 36, was reported from Webster, N. Y., 25 miles southwest from Canandaigua, between October 11 and 13. Evidently the previous flight from Canandaigua three months before, together with the view of the landscape from the airplane window, had not sufficed to permit successful orientation by visual landmarks. Numbers 4 and 16 found their way home, but No. 16 remained out overnight.

The remaining four birds flew SSE immediately after release at 4:15 P.M. with no circling at all, but were unfortunately lost to view six miles SSE from the release point when they apparently landed in a patch of woods (see Fig. 6). This relatively straight flight departed almost immediately from the area over which these birds had flown after their previous release at Canandaigua on July 25. Three birds of this group homed promptly, but No. 17 remained out overnight.

Honeoye Falls, 72 miles WNW; birds released 11:02 A.M., October 12; clear and warm, visibility eight to ten miles with slight haze, wind SSW eight to ten mph. The birds circled near the release point for 13 minutes before flying the route shown in Figure 6. Their first heading was south for four miles, but they then turned east and circled back to the release point 23 minutes after release. On their second departure to the southeast they flew considerably farther. The lone white bird, No. 9, separated from the others at the point indicated on the map and could not be followed farther. The returns from this release were very poor; three birds with excellent previous records were never heard from again (Nos. 12, 15, and 17), and the two which did return (Nos. 4 and 9) arrived somewhere between 20 and 24.5 hours after release. The remaining bird, No. 16, was reported found dead near Trumansburg on October 25 (apparently shot). It was thus close to the direct line between the release point and home (see Fig. 4).

Despite the heavy losses, it was clear that the flock followed from the air did set out in nearly the correct direction while still within two miles of the Honeoye Falls release point. The only slow returns on previous flights had occurred after releases at Interlaken, West Fayette, and Geneva, 29 to 50 miles east of Honeoye Falls. It is surely difficult to believe that even one bird had wandered by chance to the immediate vicinity of this release point at Honeoye Falls, so that the flock must have been able to select the approximate direction of home without benefit of visual landmarks.

Batavia, 100 miles WNW; birds released 1:40 P.M., October 23; clear and warm, haze in patches caused visibility to vary from four to nine miles, wind WNW, light. The birds circled for five minutes, landed in a tree near the release point for five minutes more, and then flew rather directly south along the road leading into the city of Batavia. They circled over the city and returned to the release point. They then separated, so that only the white bird, No. 9, could be followed as it circled back to the south and continued southeast along the course shown in Figure 6. The sharp turn to the east occurred as it reached a prominent four-lane highway, along which it flew for about three miles. At Pavillion it landed on a housetop and remained for the period from 78 to 117 minutes after the time of release. During this interval the visibility increased considerably as a patch of haze over Pavillion moved to the east. After leaving Pavillion along the route shown on the map, No. 9 headed in a generally westerly direction and at 168 minutes after release it again came to the same highway near Darien. Once more it turned left and flew along this highway until lost to view among a large flock of local pigeons which it joined approximately three hours after its release at Batavia.

The flight of No. 9 was the longest traced from the air, covering 54 miles during the 2¼ hours of actual cross-country flight. Despite this bird's success in all previous flights it seemed lost and disoriented towards the end of the period of observation. Yet it can be seen from Figure 6 that even in this flight the first hour constituted progress in a generally correct direction. Both birds in this final experiment had returned from Honeoye Falls in 20 to 24.5 hours, of which only between 9 and 14 hours were daylight, so that the chance of their having acquired a familiarity with the vicinity of Batavia is very remote indeed. Once again it is necessary to conclude that these pigeons could select the correct direction without reliance upon visual landmarks.

DISCUSSION

An experienced pigeon racer would immediately recognize from these case histories that my pigeons, especially the white birds, did not display the same physical stamina for long flights as his successful racers. The losses became serious at shorter distances than in the training of the best strains of racing pigeons, and the several occasions when the birds landed showed that they were not racing for home. It should be recalled, however, that my birds were intentionally deprived of the company of more experienced pigeons on any of their training flights. In most pigeon races, birds of widely differing experience, and from several lofts, are released together.

Some of the present observations indicated a tendency for the birds to follow linear landmarks such as railroads, prominent highways, and the shores of the Finger Lakes. In the releases at Willard and Burdett topographic factors seem to have led certain birds astray. Most striking, however, was the tendency for the birds to fly rather straight courses for several miles in a generally correct direction. On several occasions, as noted above, this occurred in territory where the birds had never previously been observed to fly. The "overshoot" after the first Canandaigua release is especially interesting in view of pigeon racers' reports of similar occurrences.

To explain the essentially correct direction taken in several cases one might assume that the birds had actually visited the release area after some previous release, during the excess time above that required for a direct flight home. The releases at Honeoye Falls and Batavia are good examples; for the flock took the correct initial direction within two miles of the release point. Individual birds had remained out for one to four days after releases at Interlaken, West Fayette, or Geneva. But it seems improbable that they had indulged in enough wandering to have carried them over the area immediately surrounding Honeoye Falls or Batavia. Moreover the birds often deserted the correct direction after about an hour of flying; if they were indeed familiar with the countryside one would not expect this to occur.

It should be borne in mind that all of the more distant release points in Experiment II lay nearly on a line extending approximately northwest from the home loft. The birds flew in a generally southeasterly direction after release in what was almost certainly unfamiliar territory. This could be considered either as an ability to fly towards home, or alternately as an ability to fly southeast, learned in the course of several previous flights in that direction. The obvious critical experiment of a release at 75 to 100 miles in some totally different direction was planned, but could not be carried out because of the rapid dwindling of the flock.

The possibility that the sun is used as a means of orientation by birds should not be overlooked; such a notion has become more attractive in recent years because of the remarkable discoveries of von

Frisch (1950) concerning the precise orientation of insects with reference to the sun. The results of the release at West Fayette coincide with racers' experience that heavy losses are likely to occur in the presence of a heavy overcast and poor visibility. It should also be recalled that in pigeon races of 100 miles or more it is customary to make all releases in the early morning, and furthermore to select release points at various distances so that they all lie in roughly the same direction from the home lofts. Such arrangements might possibly have been adopted empirically because they facilitated an initial orientation relative to the rising sun. In Experiment II the releases were made in the middle of day, with one or two exceptions. It had been my original plan to vary the hour of release in order to test the possibility that the sun's position was an important factor, but the heavy losses at distances beyond 50 miles made this impossible.

The relatively slight variation in time of day at which pigeons were released did not appear to be correlated with the direction of their flight except in one case. In the second release at Canandaigua on October 7, 1947, the flock of eight birds was divided into two groups of four, and the second group to be released had been held in their shipping box for somewhat longer than was usual in these experiments. The behavior of this group after release was striking in that they began a cross-country type of flight almost immediately after their release without the ten to twenty minutes of circling in the immediate vicinity of the release point that occurred in almost every other case. The hour of this release, 4:15 P.M., was distinctly later than that of any previous release at more than 20 miles (for example, the five preceding releases had been at 2:53 P.M., October 2; 9:50 A.M., September 27; 3:35 P.M., July 25; 3:01 P.M., July 23; and 11:25 A.M., July 15). The approximate heading of the pigeons during this straight flight observed from the air between 4:15 and 4:30 P.M., October 7, was 160°; this may be compared with a heading of 135° flown by the flock followed after a previous release at Canandaigua on July 25, after the birds had begun an essentially straight flight over what was probably unfamiliar territory. This shift of about 25° to the south corresponds to the sun's movement across the sky in one hour and forty minutes, a rough agreement with the time interval separating this release from the customary release time between 2 and 3 P.M. This single correlation can, however, be considered merely as a suggestive indication.

Subsequent to these observations four additional studies of pigeon homing have been reported. Hitchcock (1950, 1952) has followed flocks of U. S. Signal Corps racing pigeons or their immediate progeny over both familiar and unfamiliar territory. The greatest distance of transportation from the home loft was 190 miles. Hitchcock observed many deviations from the direct course home while following these pigeons from small airplanes — even within familiar territory. The control of previous flights was apparently less complete than in the experiments reported above, so that it is more difficult to set precise limits to the birds' familiar territory. But in three significant cases birds trained to return to their home loft in New Jersey from release points up to 100 miles to the west were carried 100 to 190 miles north and followed after release in what was certainly unfamiliar territory. In all three cases many birds headed to the east or southeast for the first 25 to 50 miles, demonstrating a tendency to take the direction of the previous training flights even though this direction led them away from home.

On the other hand, in these and other flights observed by Hitchcock some birds were clearly able to head towards home even from unfamiliar territory. In the clearest case birds were first trained by releases up to 35 miles to the northwest, 17 miles to the east, 28 miles to the southwest and 87 miles to the southeast. They were then released at Massena, N. Y., 106 miles northwest of the home loft at Middlebury, Vermont. These birds were followed over a route reminiscent of the flight paths described above at Honeoye Falls and Batavia. The general trend of the flight path clearly lay between east and south, so that these pigeons were taking the correct general direction. There was, however, one complicating geographical factor in the Massena experiment. Virtually all the previous flights of these pigeons had been in hilly or mountainous regions of Vermont or the Adirondack area of New York. Massena lies in the broad, flat valley of the St. Lawrence River, and at the time the birds were observed the Adirondack mountains were apparently visible. Hence the pigeons might possibly have been using these mountains as an ecological cue (in the meaning discussed earlier, Griffin 1944); but in view of other evidence discussed below it seems far more likely that these pigeons were in fact able to select roughtly the correct direction in unfamiliar territory.

Yeagley (1947 and 1951) has reported extensive experiments with homing pigeons designed to test a theory of bird navigation based upon an assumed sensitivity to terrestrial magnetism and to the Coriolis force. This theory has been adequately and severely criticised from several points of view (Thorpe 1949); but some of Yeagley's recent work has involved airplane observations of pigeons, both in familiar and unfamiliar territory. Again the pigeons sometimes showed wide deviations from the direct course, even within familiar territory. Fourteen birds were followed for significant distances after individual releases in totally unfamiliar territory (several hundred miles from home); thirteen of these were released at the same point and one at another point several miles to the north. Nine of the first 13 birds flew in a northwesterly direction, while the remaining four scattered in other directions. The single bird set free at a different release point also flew to the northwest. It is difficult to accept Yeagley's explanation of these flight paths for reasons made clear by Thorpe and other critics; and there does not seem to have been any clear relation between the northwesterly heading and previous training flights. The selection of the same general direction of flight by so large a proportion of these birds complements the evidence discussed above for some orienting factor that is related to *direction,* rather than to *position* of the home loft.

A third recent contribution by Kramer and his associates (Kramer and St. Paul, 1950; Kramer and Seilkopf, 1950; and Dinnendahl and Kramer, 1950) offers further support for this point of view. Pigeons released in unfamiliar territory, at some distance from the line along which previous training releases had been made, tended to start their flights in the direction of the earlier training flights; and they required longer, on the average, to reach their home than when released along the line connecting the previous release points with the home loft.

All this evidence, together with Skinner's recent demonstration (1950) of the striking ability of pigeons to retain visual memories of landmarks, suggests that orientation is based upon visual factors, but not solely upon topographic memory of familiar territory.

Matthews (1951) has recently presented a substantial contribution to the problem of pigeon navigation. Using birds raised especially for his experiments by experienced and successful racers he judged their homing performance both by the customary standards of speed and percentages of returns and also by the initial direction of flight observed through binoculars from the release point. In his earlier experiments with birds of three to four months trained up to distances of 18 miles, and trained predominantly in one direction, Matthews found that releases in unfamiliar territory tended clearly to result in flights that approximated the training direction. In this the results were similar to those reported by Kramer *et al.* and by Hitchcock. But in Matthews' later experiments with more experienced birds (training flights of 25 to 127 miles) the initial flight directions after release in unfamiliar territory centered around the true direction of home rather than approximating the training direction or scattering at random.

Matthews showed, by releases at different times of the day, that no simple insect-like flight at a fixed angle to the sun could account for even those cases where birds in unfamiliar territory did hold to the direction of their training flights. In other experiments he obtained entirely negative results from a repetition of Yeagley's experiments in which magnets attached to homing pigeons were reported to worsen their homing performance. Matthews found that on the average the homing performance of his birds was better on clear or partly cloudy days than under a solid overcast, and he is inclined towards some explanation of pigeon navigation based upon the position of the sun.

Taking all of these results into consideration we may conclude that pigeons vary so greatly in homing ability that it is advisable to distinguish three distinct levels of navigational ability. What we may conveniently call type I homing is reliance upon "contact flying" within familiar territory. When released in totally unfamiliar territory birds which exhibit only type I homing show a quantitative homing performance that can easily be accounted for by theories of exploration or even by a completely random search for familiar landmarks. They may be misled by topographic features resembling portions of their familiar territory. Clear examples would be the pigeons of Experiment I. Pigeon racers generally believe that young and inexperienced pigeons home in this way, and, among wild birds, the gannets followed by airplane gave every evidence of employing type I homing.

A second level of homing, conveniently designated type II, is the ability to maintain flight in roughly a fixed *direction,* usually that adhered to in previous training flights. Examples would be the birds from Fort Monmouth, New Jersey, followed by Hitchcock after being released in central New York State; these birds had been trained to fly east from training releases in Pennsylvania, and they were followed by air as they flew easterly courses over unfamiliar territory. The earlier experiments of Matthews and the behavior of pigeons described above after releases at Canandaigua, Honeoye Falls, and Batavia appear to be type II. Since most pigeon races involve a series of release points all lying in roughly the same direction from home, flying in a fixed direction may be of predominant importance in pigeon racing. Furthermore the results obtained with wild birds by Schüz (1934, 1949), by Rüppell (1944) and by Rowan (1946) suggest that cross-country flights in roughly a fixed direction may be of importance in the natural migrations of many wild birds.

Finally there is a third level of homing ability, conveniently designated as type III, which permits birds to fly approximately straight towards home from unknown territory *regardless of the direction in which home lies.* Such an ability has long been tacitly assigned to homing pigeons and to wild birds; but aside from unsatisfying, indirect evidence such as that obtained with petrels (Griffin, 1940), the recent work of Matthews with pigeons affords the first rigorous evidence for the existence of this third and most remarkable type of homing. In addition, at least one of the pigeon flights traced from the air by Hitchcock appears to fall into type III. Most recently of all, Kramer and von St. Paul (1952) have reported two additional cases of type III homing in pigeons.

In differentiating between these three types of homing one must not forget that the same flock of pigeons may exhibit two, or even all three, of these types of orientation at different times during a single homing flight. Thus Hitchcock's birds which had been trained to fly east and were then released in unfamiliar territory did follow an easterly course that continued for an hour or two. But then they shifted to a different, and usually a more correct, direction, perhaps because the flight in the direction of previous training had not brought any familiar landmarks into view. These birds appear to have used type II homing at first and then shifted to something approximating type III. Pigeon No. 9 released at Batavia followed a route, described above, which suggests type II homing during the first hour, followed, after failure to reach familiar territory, by type I.

In conclusion, it must be admitted that the central problem of pigeon navigation remains unsolved; the sensory basis of orientation in both type II and type III homing is still a matter for speculation. There is, however, good reason to hope that the real progress achieved within the past few years will continue during the reasonably near future, and that the definite demonstration of these three categories of homing in pigeons may lead to their further analysis, and eventually to experiments that will clarify the sensory basis of types II and III. Indeed significant progress in this direction has been reported very recently by Kramer and his associates, who have apparently succeeded in arranging an experimental situation in which birds demonstrate their choice of a definite compass direction while confined within a small cage. The results achieved to date point towards a sort of celestial navigation based upon the sun and sky brightness patterns; but a discussion of this subject is outside the scope of the present paper, especially since the current status of the larger subject of orientation in wild birds as well as pigeons has recently been reviewed elsewhere (Griffin, 1952).

BIBLIOGRAPHY

CLAPARÈDE, E.

1903. La faculté d'orientation lointaine. Arch. de Psychol., Geneva, **2**: 133–180.

EXNER, S.

1905. Über das Orientierungsvermögen der Brieftauben. Sitzungsber. Kaiser. Akad. Wiss. Wien, Math.-Naturwiss. Kl. III, **114**: 763–790.

DINNENDAHL, L., and G. KRAMER

1950. Heimkehrleistungen italienischer und deutscher Reisetauben. Die Vogelwarte, **15**: 237–242.

FRISCH, K. v.

1950. Bees, their vision, chemical senses, and language. Cornell Univ. Press, Ithaca, N. Y.

GRIFFIN, D. R.

1940. Homing experiments with Leach's petrels. Auk, **57**: 61–74.

1943. Homing experiments with herring gulls and common terns. Bird Banding, **14**: 7–33.

1944. The sensory basis of bird navigation. Quart. Rev. Biol., **19**: 15–31.

1952. Bird navigation. Biol. Rev., **27** (4): in press.

GRIFFIN, D. R., and R. J. HOCK

1949. Airplane observations of homing birds. Ecology, **30**: 176–198.

GUNDLACH, R. H.

1932. A field study of homing in pigeons. Journ. Comp. Psychol., **13**: 397–402.

HEINROTH, O., and K. HEINROTH

1941. Das Heimfinde-vermögen der Brieftauben. Journ. f. Ornithol., **89**: 213–256.

HITCHCOCK, H. B.

1950. Aerial observations of homing pigeons. Anat. Rec. **108**, (3): 571–572.

1952. Airplane observations of homing pigeons. Proc. Amer. Philos. Soc., **96**: 270–289.

HODGE, C. F.

1894. The method of homing pigeons. Popular Science Monthly, **44**, (April): 758–775.

KRAMER, G.

1952. Experiments on bird orientation. Ibis, **94**: 265–285.

KRAMER, G., and U. v. ST. PAUL

1950. Ein wesentlicher Bestandteil der Orientierung der Reisetaube: Die Richtungsdressur. Zeitschr. f. Tierpsychol., **7**: 620–631.

1952. Heimkehrleistungen von Brieftauben ohne Richtungsdressur. Zool. Anz. Suppl. Bd., **16**: 172–178.

Kramer, G., and H. Seilkopf

1950. Heimkehrleistungen von Reisetauben in Abhängigkeit vom Wetter, insbesondere vom Wind. Die Vogelwarte, **15**: 242–247.

Matthews, G. V. T.

1951. The experimental investigation of navigation in homing pigeons. Journ. Exp. Biol., **28**: 508–536.

Platt, C. S., and R. S. Dare

1945. The homing instinct in pigeons. Science, **101**: 439–440.

Rabaud, E.

1928. How animals find their way about. (Chap. V.), Harcourt, Brace and Co., N. Y.

Rivière, B. B.

1929. "The homing faculty" in pigeons. Proc. Sixth Int. Ornithol. Congr. Copenhagen, 1926: 535–555.

Rowan, W.

1946. Experiments in bird migration. Proc. and Trans. Roy. Soc. Canada, (3) **40**, sect. 5: 123–135.

Rüppell, W.

1944. Versuche über Heimfinden ziehender Nebelkrähen nach Verfrachtung. Journ. f. Ornithol., **92**: 106–132.

Schüz, E.

1934. Vom Storch-versuch 1933 der Vogelwarte Rossitten. Der Vogelzug **5**: 21–25.

1949. Die Spät-Auflassung ostpreussischer Jungstörche in Westdeutschland durch die Vogelwarte Rossitten 1933. Die Vogelwarte **15**, (2): 63–78.

Skinner, B. F.

1950. Are theories of learning necessary? Psychol. Rev., **57**: 193–216.

Thorpe, W. H.

1949. Recent biological evidence for the methods of bird orientation. Proc. Linnean. Soc. London, **160**: 85–94.

Watson, J. B., and K. S. Lashley

1915. Homing and related activities of birds. Papers Dept. Marine Biol. Carnegie Instit., **7**: 1–104. (Carn. Inst. Publ. No. 211)

Yeagley, H. L.

1947. A preliminary study of a physical basis of bird navigation. Journ. Appl. Physics, **18**: 1035–1063.

1951. A preliminary study of a physical basis of bird navigation, II. Journ. Appl. Physics, **22**: 746–760.

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PRINTED FOR THE MUSEUM
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No. 9 — *The Apseudid Chelifera of the Eastern Tropical and North Temperate Pacific Ocean*[1]

By Robert James Menzies

Research Fellow, Allan Hancock Foundation
The University of Southern California

INTRODUCTION

The crustacean order Tanaidacea (auct. Chelifera) has for many years been considered to be constituted by the families Apseudidae and Tanaidae. The recent subdivision of the Tanaidae by Lang (1949) into the Tanaidae (*sensu stricto*), and the Paratanaidae suggests that a further division of the Apseudidae may also be in order, since it too is composed of a heterogeneous group of genera. Currently, however, there is no good evidence that a splitting of the Apseudidae can be made successfully, because the characteristics of too many of its genera and species are imperfectly known.

The only monographic account treating American Tanaidacea is Richardson's (1905) "A Monograph on the Isopods of North America", in which the Tanaidacea are considered a suborder of the Isopoda. This lumping of the tanaids and isopods into one order represents an outdated classification; however, because one finds that classification in use today it seems desirable that a few of the major differences between the tanaids and isopods be pointed out.

In the Tanaidacea a carapace is present. This consists of a fusion of the first peraeonal somite with the cephalon. Contained within the carapace in a branchial chamber are the "cephalic" gills which consist of delicate, foliaceous appendages attached to the maxillipeds. The peraeon consists of only six free somites. The first pair of peraeopods, which are attached below the carapace, are invariably chelate. The eyes are usually located on eyelobes which are separated from the carapace. The rami of the uropods are multiarticulate. In complete contrast, the Isopoda have no carapace and no cephalic gills, although in some species the first peraeonal somite does fuse with the cephalon. Respiration in the Isopoda is carried out by means of foliaceous appendages called pleopods which are attached in pairs to the somites of the abdomen or pleon. The first pair of peraeopods of isopods is never chelate although in a few genera, those of the Anthuridae particularly, subchelate peraeopods occur. The eyes of the isopods are invariably fused with the head, and separated eyelobes are not known to occur. The rami of the uropods are usually flattened; each ramus consists of a single article.

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The first species to be described from the area under consideration were *Apseudes meridionalis* Richardson (1912a) and *Apseudes tropicalis* Richardson (1912b). Both were collected from below 400 fathoms, the former, off the Galapagos Is., and the latter from off Cape San Lorenzo, Ecuador. These species have not been recorded since. Until the discovery of *Dalapseudes* (Boone 1923), a probable synonym of *Parapseudes*, at Laguna Beach, California, not a single record existed of an apseudid from the Pacific shores of North America. The discovery of *Synapseudes intumescens* Menzies (1949) from Dillon Beach, Marin County, California, brought the number of previously known species from the area under consideration to four.

The writer has examined numerous collections of Tanaidacea from localities north of California. None contained specimens of apseudids and to date these animals are not known from Alaska to the southern border of Oregon. In localities in California and points south apseudids do not seem to be rare. About the only factors which might account for their obscurity up to the present time are their small size and a paucity of investigators interested in the group.

Seven genera are characterized in this paper. Two are described as new. Five of the genera are new to the fauna of the region. Seventeen species are considered in this paper, of which thirteen are described as new to science.

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figures. The assistance of the Museum of Comparative Zoology in the publication of this paper is particularly appreciated.

Key to the Families of the Tanaidacea

A. First antenna without an accessory flagellum.
  B. Marsupium formed of one pair of oostegites which proceed from the proximal inner margin of the fifth pair of peraeopods. . . . . *Tanaidae**
  B¹. Marsupium formed by four pairs of oostegites which proceed from the proximal inner margin of the second to fifth pairs of peraeopods. . . . . *Paratanaidae**
A¹. First antenna with an accessory flagellum. . . . . *Apseudidae*

Family APSEUDIDAE

As can be seen from the key, the Apseudidae may be told from the Tanaidae and Paratanaidae due to their having an accessory flagellum on the first antenna. In addition, they usually have a scale attached to the second antenna and often have a triarticulate epipod attached to the first (gnathopod) and second pairs of peraeopods. The antennal scale and epipods are absent from the Tanaidae and Paratanaidae.

Key to the Genera of Apseudidae Known from the Eastern Tropical and North Temperate Pacific Ocean

A. Second antenna without a scale.
  B. Pleon with three somites including telson. . . . . . . *Synapseudes* (p.461)
  B¹. Pleon with six somites including telson. . . . . . . *Pagurapseudes* (p.470)
A¹. Second antenna with a scale.
  B. Mandibular palp with less than three articles. . *Kalliapseudes* (p.471)
  B¹. Mandibular palp triarticulate.
    C. First somite of pleon much narrower than other somites of pleon . . . . *Imitapseudes* n. gen. (p. 482)
    C¹. Somites of pleon all of similar width.
      D. Adult with five pairs of pleopods.
        E. Gnathopod (first peraeopod) of adult with an epipod . . . . *Apseudes* (p.446)
        E¹. Gnathopod of adult without an epipod. . . . . *Cyclopoapseudes* n. gen. (p.489)
      D¹. Adult with four pairs of pleopods. . . . . *Parapseudes* (p.456)

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* Not treated in this paper. Characteristics after Lang (1949).

Genus APSEUDES Leach

Synonyms. Apseudes Leach, 1814, p. 404.
Eupheus Risso, 1816, p. 124.
Rhoëa Edwards, H. Milne, 1828, p. 292.

Type species. Cancer Gammarus Talpa Montagu, 1808, pp. 98–99, pl. IV, fig. 6.

Diagnosis. Pleon consisting of six somites including the telson. Adult with five pairs of pleopods. Gnathopod and second peraeopod with an epipod. Second antenna with a scale. Mandibular palp triarticulate. Dactyl of second peraeopod with a simple, pointed apex. Somites of pleon all of similar width. Separated eyelobes, with or without facets, present or absent.

Remarks. The two species of *Apseudes* which Richardson described from the Galapagos and Ecuador were not represented in the collections which I have examined. To date the genus has not been recorded from the coastal area between Point Barrow, Alaska, and San Diego, California.

Key to the Species of Apseudes

A. Each lateral border of the telson with two to five spinelike lateral extensions.
  B. Four to five lateral extensions present on each side of the telson.... .... *meridionalis* Richardson
  B¹. Two lateral extensions present on each side of the telson.......... .... *galapagensis* Richardson
A¹. Lateral borders of telson lacking spinelike extensions.
  B. Eyelobes lacking.................................. *pernix* n. sp.
  B¹. Eyelobes present.
    C. Eyelobes with facets and pigment .... *garthi* n. sp.
    C¹. Eyelobes lack facets and pigment .... *cedroensis* n. sp.

APSEUDES MERIDIONALIS Richardson

Figure 1A

Apseudes meridionalis Richardson, 1912a, pp. 583–585, 1 text-fig.

Diagnosis. Richardson describes the diagnostic telson as follows: "The sixth or terminal segment is 4 mm. long; at the place of attachment of the uropods it is 1½ mm. wide; at its anterior extremity it is provided with a strong spine, and just behind the middle, with three long spines on either side of the lateral margin; on one side there is a fourth spine in front of the three lateral spines. On the dorsal surface just within the anterior lateral spines are two small spines, one on either side of the median line, and behind these at about the middle of the segment are two other small spines, one being larger and more conspicuous than the other."

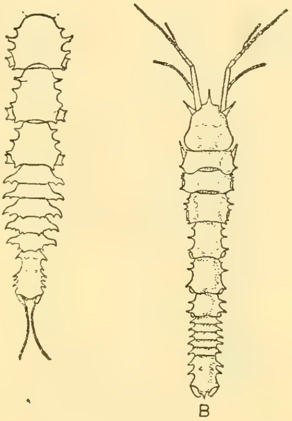

Fig. 1. *A. Apseudes meridionalis* Richardson, posterior half of body X 4⅔ (after Richardson 1912), B. *Apseudes galapagensis* Richardson, magnification not known (after Richardson, 1912).

Remarks. The type and only specimen of this species consists of the last three peraeonal somites and the pleon; therefore, nothing is known of the anterior peraeonal or cephalic structures. Richardson did not describe the structure of the pleopods or posterior pairs of peraeopods. It might be questioned whether the species is a true *Apseudes.* The peculiar structure of the pleon and telson is characteristic and if the species is an *Apseudes* then it probably is valid.

Type locality. Off Cape San Lorenzo, Ecuador, March 2, 1888 (lat. 00° 37′ 00″ S.; long. 81° 00′ 00″ W.) at a depth of 401 fms., in green mud. Collected by the U. S. Bureau of Fisheries Steamer "Albatross". (Richardson 1912a, p. 584).

Location of type. The type is located in the United States National Museum, Washington, D. C., Cat. No. 43504.

Geographic range. Known only from the type locality.

APSEUDES GALAPAGENSIS Richardson

Figure 1B

Apseudes galapagensis Richardson, 1912b, pp. 159–161, figs. 1–2.

Diagnosis. Separated eyelobes present, each with a long, anteriorly directed spine; eyes absent. Outer branch of first antenna with fourteen articles, inner branch with six articles. Second antenna with thirteen articles; scale present. Immovable finger of gnathopod with a triangulate tooth near the articulation of dactyl with propod. Telson "about as long as the four preceding segments taken together; it terminates in an acute point which is upturned. About the middle of the dorsal surface are two spines, one on either side of the median line. The lateral margin is produced on either side in two long, acute processes, one a little below the middle of the segment and the other a little above" (Richardson 1912b, p. 160).

Measurements. None given.

Type locality. Off Chatham Island, Galapagos Islands, April 4, 1888 (Sta. 2807, U. S. Bur. Fish. "Albatross"), depth 812 fms., in globigerina ooze, coral and mud, one specimen (Richardson 1912b, p. 161).

Location of type. The type is located in the U. S. National Museum, Washington, D. C., Cat. No. 43694.

Geographic range. Known only from the type locality.

Remarks. Richardson neither figures nor describes the mouth parts and her description of the peraeopods is inadequate.

APSEUDES GARTHI new species

Figure 2

Diagnosis. Rostral area triangulate sharply pointed. Facet bearing separated eyelobes present, extending onto the dorsal surface of the cephalon. Ocular spines lacking. Medial margin of first article of first antenna with small spines. Inner branch of flagellum of first antenna with two articles; outer with six. Second antenna with ten articles; scale with four apical setae. Immovable finger of gnathopod of male with a triangulate tooth near the articulation of dactyl with propod. Telson as long as the four preceding somites of pleon. Lateral margins of telson bilobate; terminal area between uropods triangulate; dorsal surface lacking spines or spine-like processes. Uropods slightly longer than pleon; exopod with five articles, endopod with thirteen articles. Maxilliped with one coupling hook. Branches of pleopods uniarticulate.

Measurements. Female holotype, length 1.9 mm., width 0.27 mm.

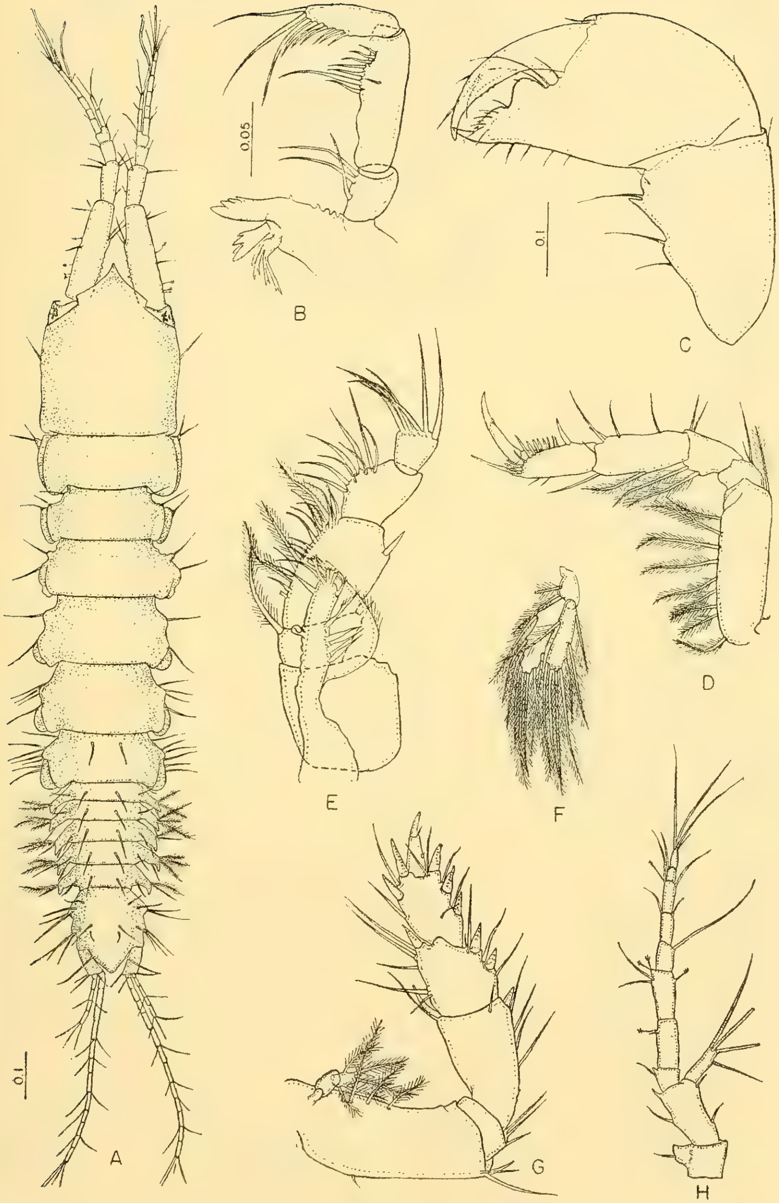

Fig. 2. *Apseudes garthi*, n. sp., holotype. A. toto, B. left mandible, C. gnathopod of male paratype, D. seventh peraeopod, E. maxilliped, F. second pleopod, G. second peraeopod, H. second antenna. Figures with similar magnification, A; B, E; C, D, F, G, H.

Type locality. San Gabriel Bay, Espiritu Santo Island, Gulf of California, Mexico, March 15, 1949, holotype, from coral heads, AHF Sta. No. 1737–49, with specimens of *Parapseudes pedispinis* (Boone).

Location of type. The holotype is deposited in the collections of the Allan Hancock Foundation, Cat. No. 4911.

Material examined (exclusive of type). Isabel Island, Sinaloa, Mexico, March 19, 1933, 2 specimens from coral, AHF Sta. No. 125–33. These specimens have been designated as paratypes. They are deposited in the collections of the U. S. National Museum, Washington, D. C.

Geographic range. Gulf of California, Mexico, Isabel Island to Espiritu Santo Island.

Remarks. Apseudes garthi appears to resemble *A. intermedius* Hansen (1895, pp. 49–50, pls. 5–6) more closely than it does any other species. It differs from *A. intermedius* in having pronounced lateral angles at the base of the rostrum and in lacking the forward projecting antero-lateral borders of the first free somite of the peraeon of *A. intermedius.*

APSEUDES PERNIX new species

Figures 3–4

Diagnosis. Rostral area triangulate, bluntly pointed. Eyes and separated eyelobes lacking. Medial margin of first article of first antenna without spines. Inner branch of flagellum of first antenna with four articles, outer branch with twelve. Second antenna composed of eleven articles; scale with nine marginal setae. Immovable finger of gnathopod with a large sharp tooth on its cutting edge; dactyl with a similar tooth located near the articular margin. Telson as long as the four preceding somites of the pleon; lateral margin of telson unilobate. Distal margin of telson slightly trilobate; dorsal surface lacking spines or spine-like processes. Uropods about one half as long as the body; exopod with eight articles, endopod with about thirty-two articles. Maxilliped with four coupling hooks. Endopod of pleopods with two articles, exopod with one.

Measurements. Male holotype, length 3.4 mm., width 0.4 mm.

Type locality. La Plata Island, Ecuador, January 22, 1933, holotype male and one paratype male, AHF Sta. No. 22-33.

Location of types. The types are deposited in the collections of the

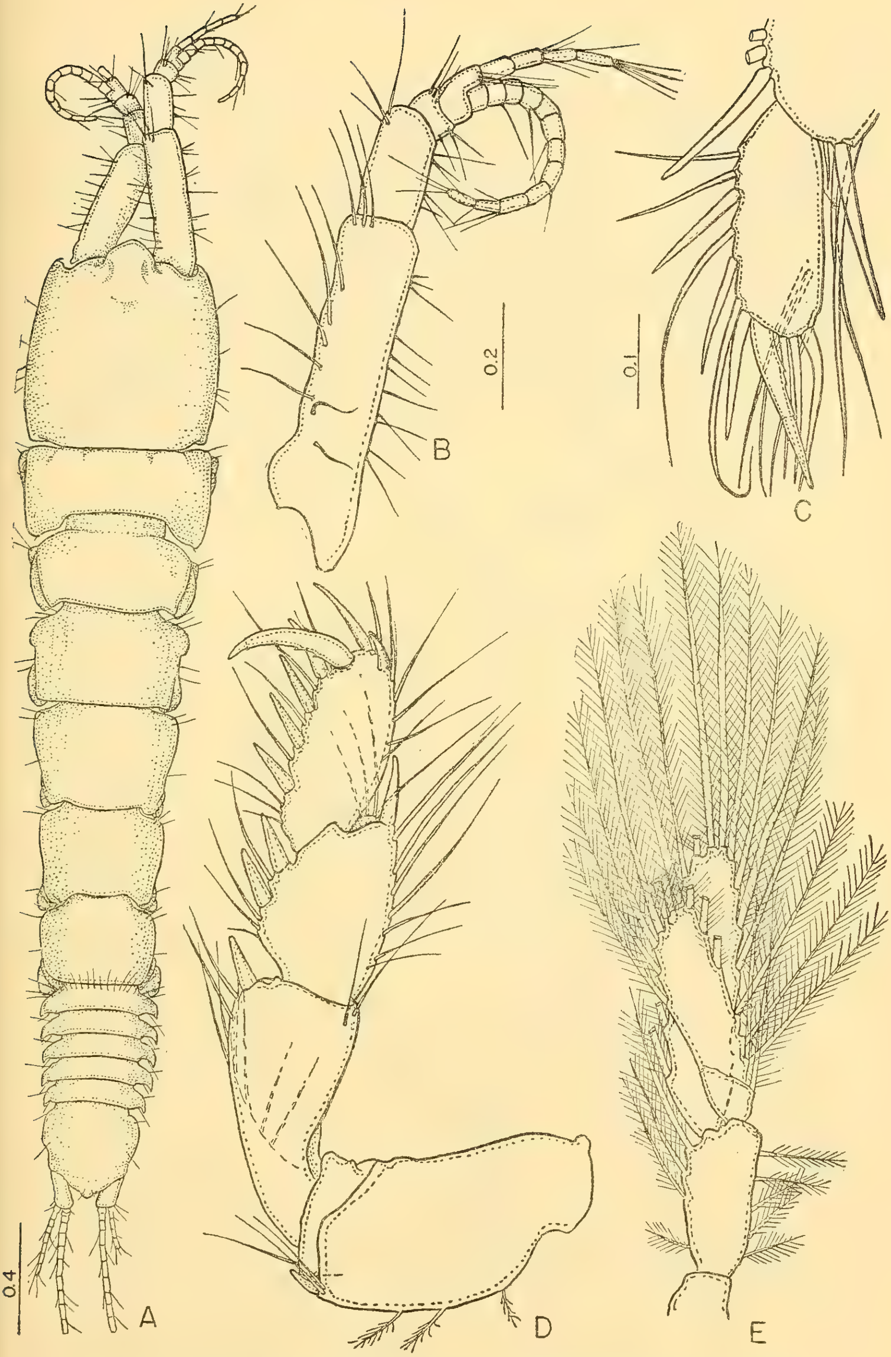

Fig. 3. *Apseudes pernix*, n.sp., holotype, A. toto, B. first antenna, C. apical joints of third peraeopod, D. second peraeopod, E. first pleopod. Figures with similar magnification, A; B, D; C, E.

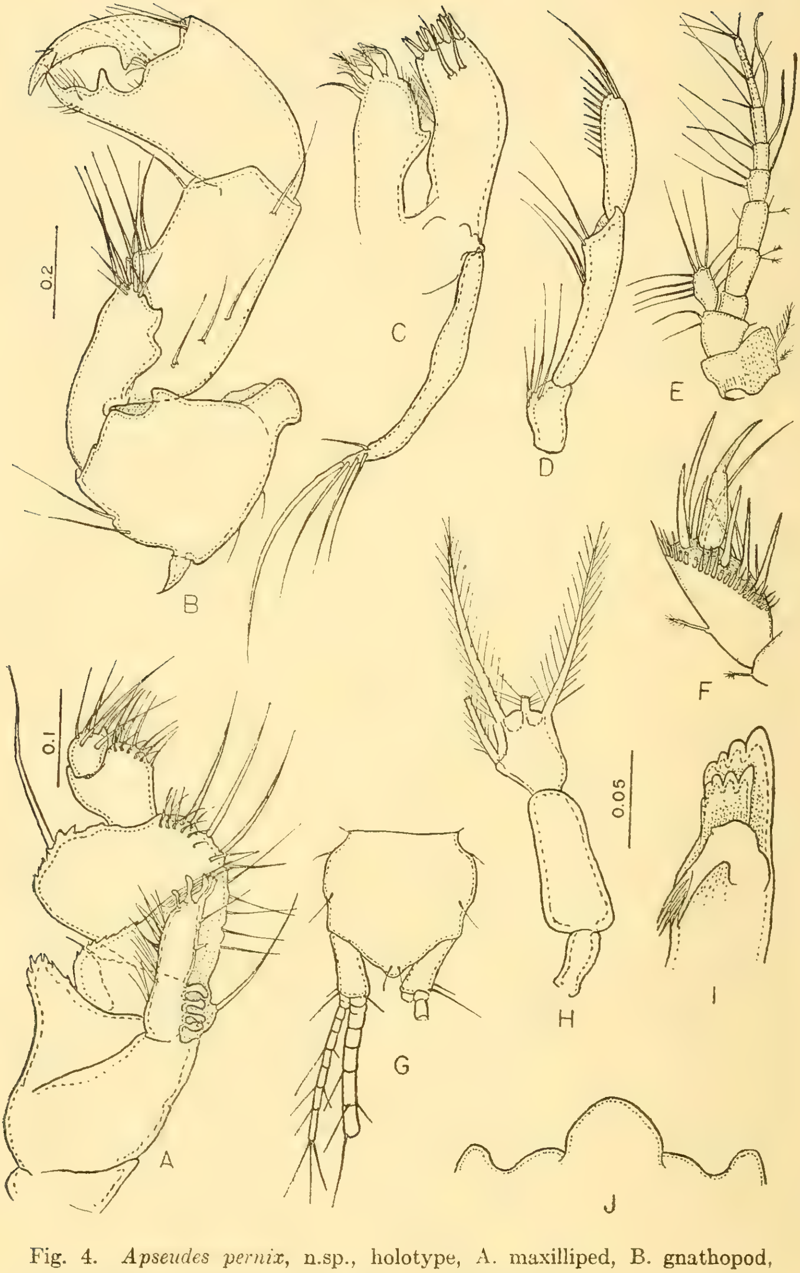

Fig. 4. *Apseudes pernix*, n.sp., holotype, A. maxilliped, B. gnathopod, C. first maxilla, D. mandibular palp, E. second antenna, F. dactyl and propod of seventh peraeopod, G. telson and uropods, H. epipod of second peraeopod, I. inner surface of left mandible, J. frontal margin of cephalon. Figures with similar magnification, A, C, D, F; B, E, G, J; H, I.

U. S. National Museum, Washington, D. C.

Material examined. Types only.

Geographic range. Known only from the type locality.

Remarks. This species shows no close affinity with any of the described species. It resembles *A. espinosus* Moore (1901, pp. 164–165, pl. 7) in general form but, unlike that species, it lacks eyes and separated eyelobes. It resembles *A. caeca* Willemöes-Suhm (1879, pp. 23–24, pl. XII) in the lack of eyes and separated eyelobes but it differs markedly from that species in lacking the sharply pointed rostrum and cephalic spines.

APSEUDES CEDROENSIS new species

Figures 5–6

Diagnosis. Rostral area triangulate. Separated eyelobes large, extending into dorsal surface; facets lacking. Medial margin of first article of first antenna with numerous small spines. Inner branch of flagellum of first antenna with five articles, outer branch with nine articles. Second antenna composed of eleven articles; scale with seven marginal setae. Immovable finger of gnathopod with a large sharp tooth on its cutting edge; dactyl with a similar tooth not far from articular margin. Telson as long as the four preceding somites of the pleon; lateral margin of telson not lobed. Distal margin of telson with one medial lobe; dorsal surface lacking spines or spine-like processes. Uropodal exopod with seven to eight articles; endopod with twenty-five to twenty-six articles; maxilliped with four coupling hooks. Endopod of pleopods with two articles, exopod with one.

Measurements. Male holotype, length 7.0 mm., width 1.0 mm. Allotype, female, length 7.5 mm., width 1.0 mm.

Type locality. South Bay, Cedros Island, Lower California, Mexico, April 19, 1951, holotype, allotype, and two paratypes, 16–19 fathoms, AHF Sta. Nos. 2026–51.

Location of types. The types are deposited in the collections of the Allan Hancock Foundation, Cat. No. 511, 511a.

Material examined. Types only.

Geographic range. Known only from type locality.

Remarks. This species appears related to *Apseudes espinosus* Moore (1901, pp. 164–165, pl. 7), from which it differs in having a pronounced median lobe at the apex of the telson, in having evident spines on the

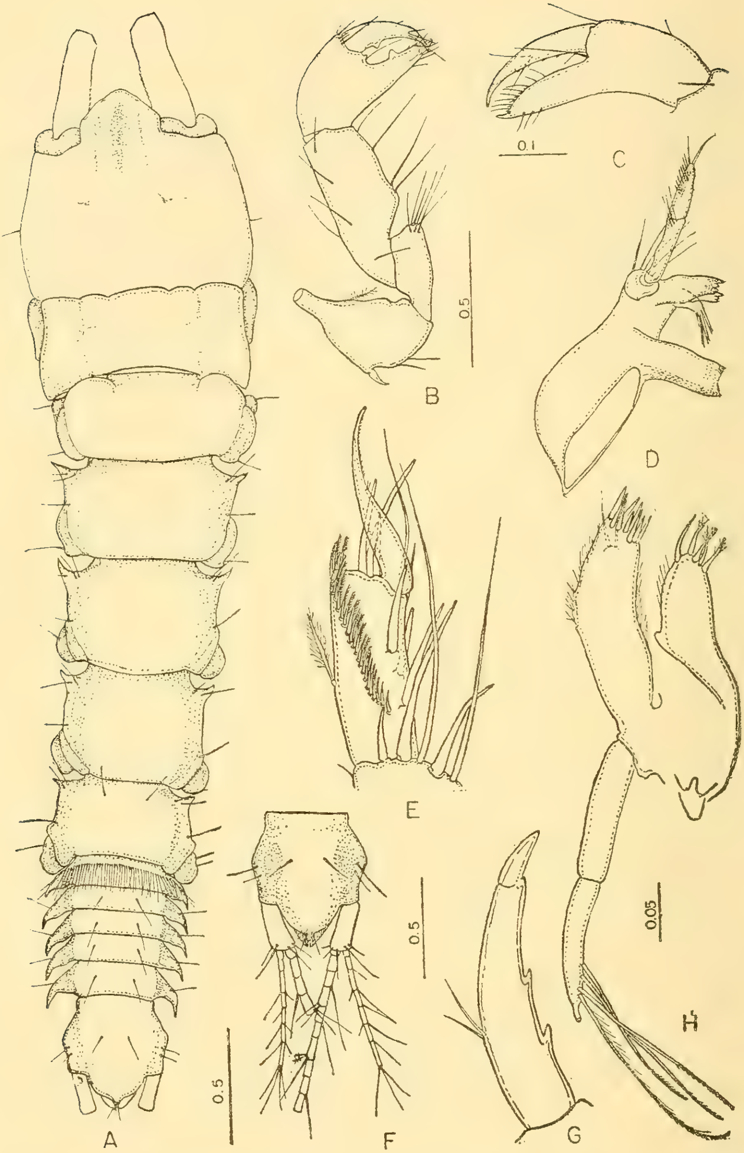

Fig. 5. *Apseudes cedroensis*, paratype male. A. toto, B. gnathopod, C. gnathopod, female, D. left mandible, E. apical articles seventh peraeopod, F. telson, G. dactyl, seventh peraeopod, H. first maxilla. Figures with similar magnification, A; B; C, D; E, G, H; F.

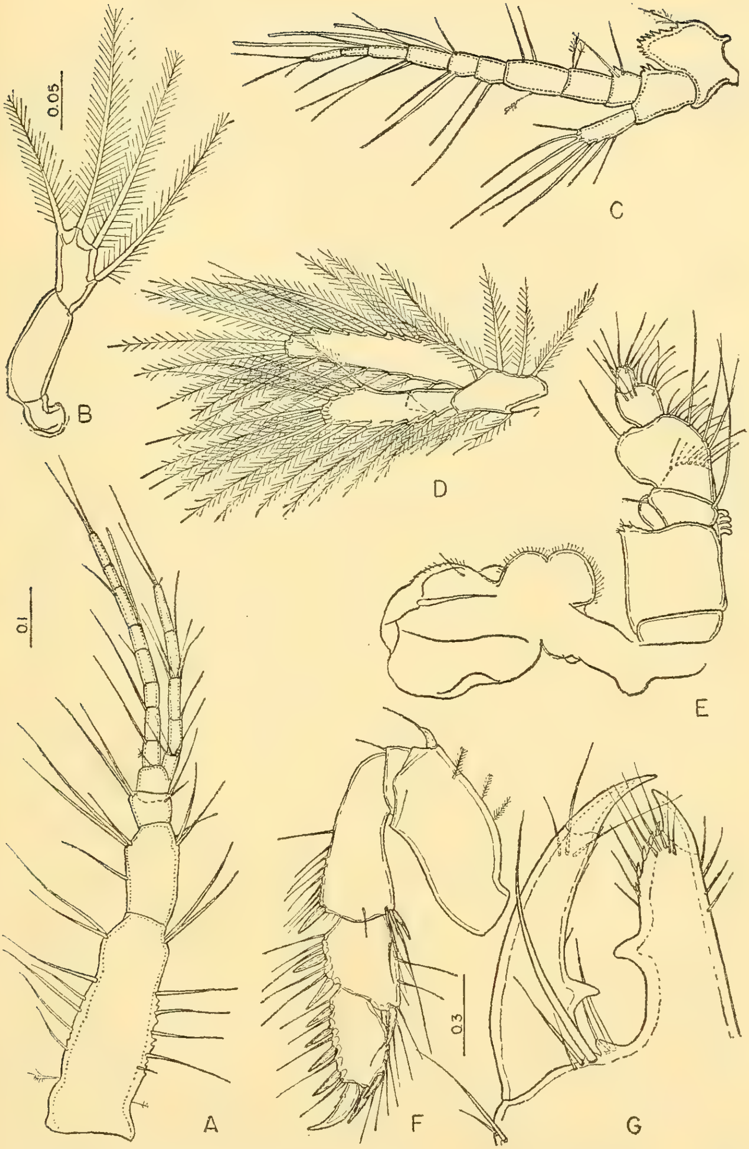

Fig. 6. *Apseudes cedroensis*, paratype male. A. first antenna, B. epipod of gnathopod, C. second antenna, D. first pleopod, E. maxilliped, F. second peraeopod, G. apex of gnathopod. Figures with similar magnification, A, D, E; B, C, G; F.

peraeonal somites, and in having much fewer articles comprising the branches of the first antennae.

Genus PARAPSEUDES G. O. Sars

Synonyms. Parapseudes G. O. Sars, 1886, p. 303.
Dalapseudes Boone, 1923, pp. 147–148.
Type species. Rhoëa latifrons Grube, 1864, p. 75.

Diagnosis. Pleon consisting of six somites including telson. Adult with four pairs of pleopods. Gnathopod and second peraeopod with an epipod. Second antenna with a scale. Mandibular palp with three articles. Dactyl of second paraeopod sharply pointed, lacking setae.

Remarks. The species assigned to this genus, except perhaps for Grube's *P. latifrons,* which was redescribed by G. O. Sars, are imperfectly known. Those which probably belong to the genus are *P. latifrons* (Grube), *P. goodei* Richardson (1902, pp. 283—284, pl. XXXVII), *P. similis* Vanhöffen (1914, pp. 462—463, fig. 3), *P. pedispinis* (Boone) (1923, pp. 147—148), and *P. neglectus* Miller (1940, pp. 309--311, fig. 5). *P. hirsutus* Stebbing (1910, pp. 89--90) should be transferred to another genus, perhaps to *Apseudomorpha* Miller (1940, p. 315) with which genus it agrees in general aspect and in the lack of pleopods and epipods.

The type of *Dalapseudes pedispinis* is located at the United States National Museum, Washington, D. C. It consists of a mutilated specimen which lacks most of its appendages, including some of the mouthparts and the uropods. This specimen closely resembles *Parapseudes* in general form and in all probability belongs to that genus. Boone's description is inadequate in several instances. She describes the four pairs of paraeopods following the gnathopods as "similar in structure." This is true of the Apseudidae only in the broad sense that the peraeopods have a similar number of articles. That she found no scale on the second antenna is not too remarkable because the second antennal scale of *Parapseudes* is small and could be overlooked easily. The presence of "epipodytes" on the last five pairs of legs, a feature mentioned by Boone in both the generic and specific descriptions, is of some interest. It seems certain that she is referring here to oostegites and not to the structures which are called epipods in this paper. This is indicated for several reasons; first, her "epipodytes" are located medial to the legs, as are oostegites and second, these "epipodytes" are equal in number to the five pairs of oostegites present in this species. Also, epipods (as the term is used in this paper) are not known to occur on the last five pairs of legs in any known apseudid.

PARAPSEUDES PEDISPINIS (Boone)

Figures 7–9

Synonyms. Dalapseudes pedispinis Boone, 1923, pp. 147–148 (a probable synonym).

Diagnosis (from specimens examined, not from Boone's description or from the holotype). Eyelobes separated from cephalon and extending onto the dorsal surface; each with about ten facets. Peduncle of first antenna with three articles; first thick, about two times the length of second. Inner branch of flagellum with seven to eight articles; outer with six to seven articles. Second antenna with eleven or twelve articles. Posterior margin of telson trilobate. Maxilliped with two coupling hooks. Epipod of gnathopod with three articles, apical article with six plumose setae on distal margin.

Measurements. One male (not holotype) 3.4 mm. in length and 0.8 mm. in width; ovigerous female, length 3.5 mm., width 0.8 mm.; figured specimen, length 4.3 mm., width 1.0 mm. (Boone did not give measurements but the holotype is similar in size to other specimens which I have seen).

Type locality. Laguna Beach, California, collected by Dr. William A. Hilton (Boone, 1923, p. 148).

Location of type. The holotype is in the collections of the U. S. National Museum, Washington, D. C.

Material examined. CALIFORNIA. *Laguna Beach,* holotype. *La Jolla,* November 1, 1949, 6 specimens, on *Phyllospadix,* R. J. Menzies. One mi. NW of White Cove, *Santa Catalina Island,* August 4, 1941, 49 specimens, on the algae *Lithothrix, Eisenia,* and *Macrocystis,* AHF Sta. No. 1378–41. Four mi. east of landing, *Santa Barbara Island,* August 28, 1941, 76 specimens, 40 fms,. AHF Sta. No. 1398–41.

MEXICO. Gulf of California, *Isabel Island,* March 19, 1933, 1 ovig. female, on coral, AHF Sta. No. 125–33. *Turner's Island,* south of Tiburon Island, January 24, 1940, 1 male, AHF Sta. No. 1042–40.

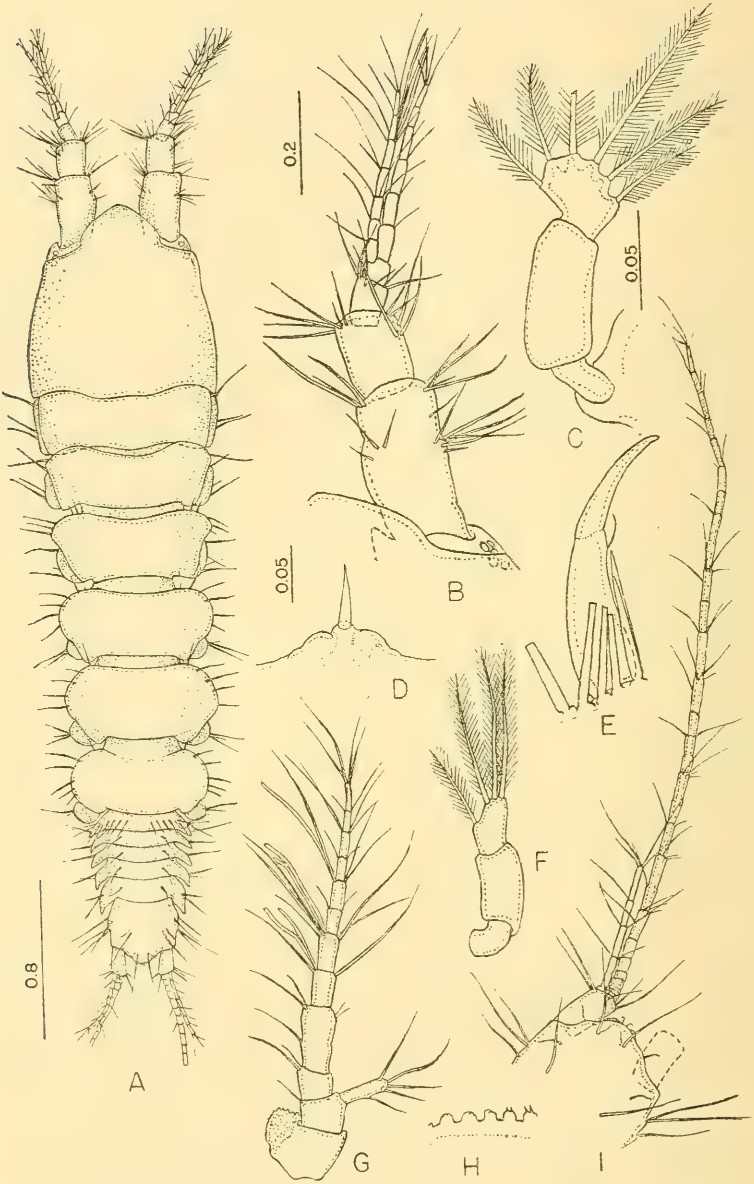

Fig. 7. *Parapseudes pedispinis* (Boone), male, A. toto, B. first antenna and eye, C. epipod of second peraeopod, D. penis, E. dactyl of seventh peraeopod, F. epipod of gnathopod, G. second antenna, H. distal margin of first article of second antenna, I. telson and uropod. Figures with similar magnification, A; B, G, I; C, E, F, H; D.

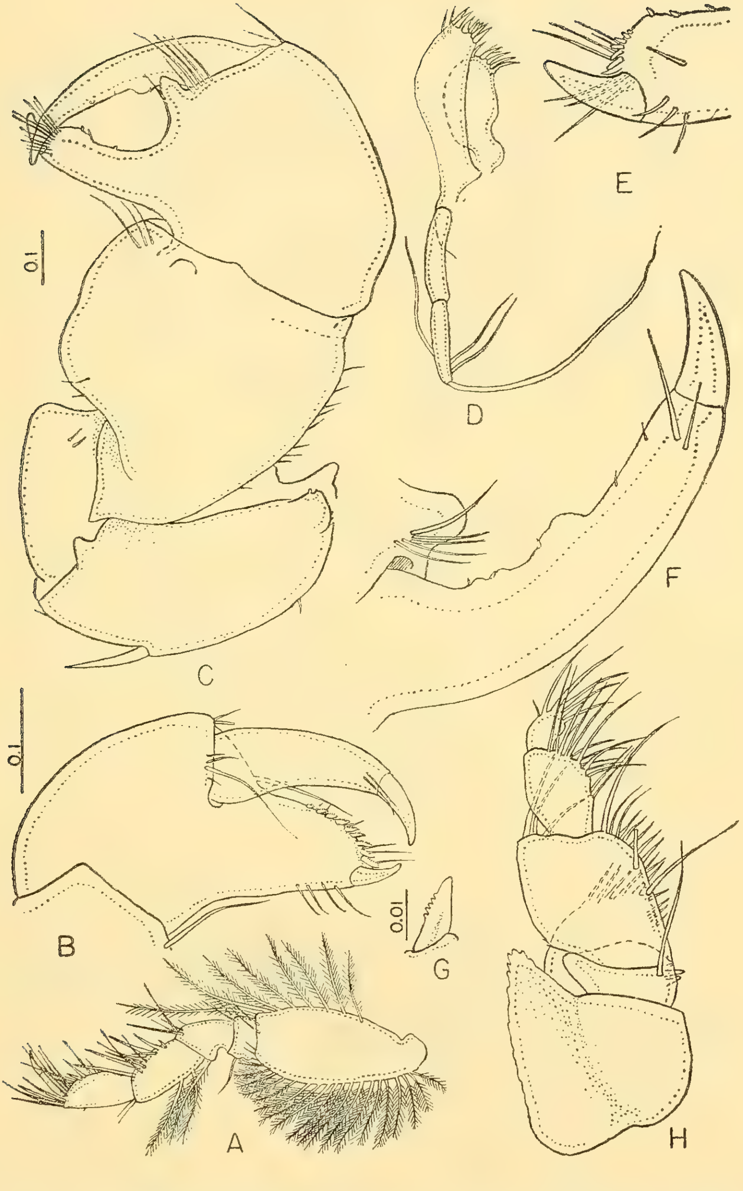

Fig. 8. *Parapseudes pedispinis* (Boone), A. seventh peraeopod, B. female gnathopod, C. male gnathopod, D. first maxilla, E. apex of immovable finger of male gnathopod, F. dactyl of male gnathopod, G. seta of superior margin of immovable finger of female gnathopod, H. maxilliped. Figures with similar magnification, A, C; B, D, E, F, H; G.

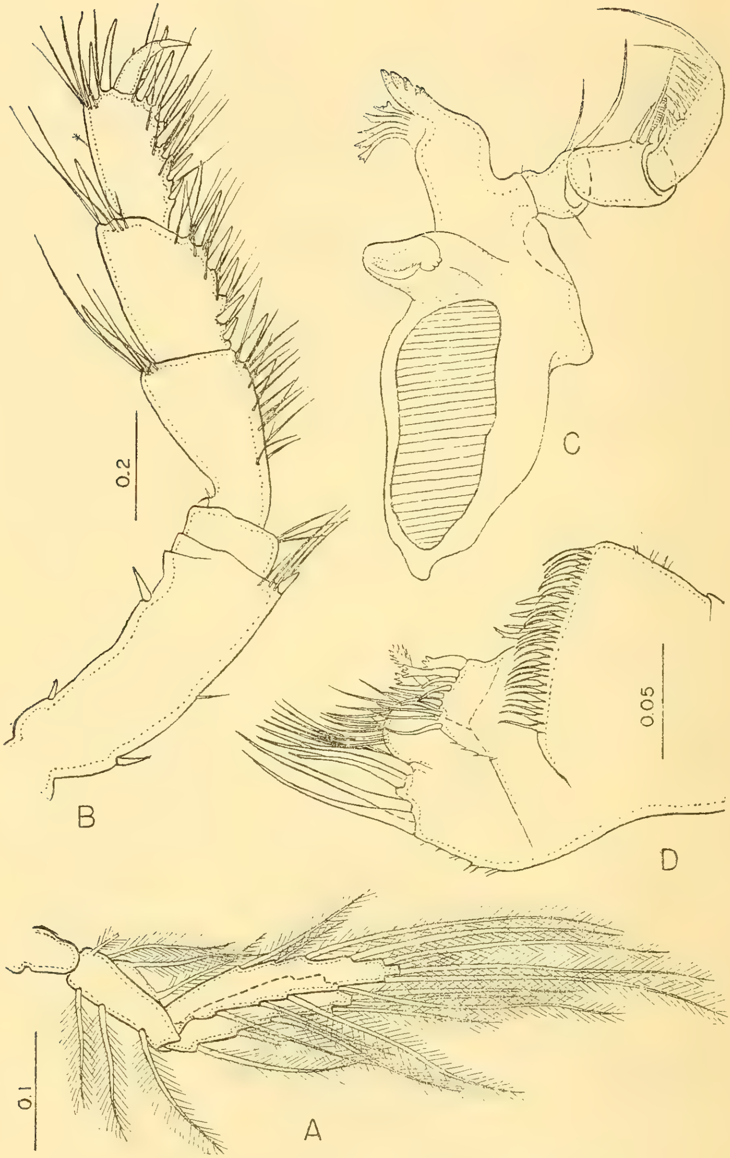

Fig. 9. *Parapseudes pedispinis* (Boone), male, A. first pleopod, B. second peraeopod, C. right mandible, D. second maxilla. Figures with similar magnification, A, C; B, D.

San Gabriel Bay, Espiritu Santo Island, March 15, 1949, 31 specimens, from coral heads, AHF Sta. No. 1737–49, with *Apseudes garthi.*

COSTA RICA. *Parker Bay*, February 9, 1935, 50 specimens, on coral, AHF Sta. No. 473–35. *Playa Blancas*, February 8, 1935, 1 male, 3–5 fms., AHF Sta. No. 460–35.

COLOMBIA. *Octavia Bay*, January 28, 1935, 1 male, on coral, AHF Sta. No. 435–35. *Gorgona Island*, February 12, 1934, 1 male, on coral, AHF Sta. No. 222–34; January 22, 1935, 26 specimens, on *Pocillopora*, AHF Sta. No. 411–35.

ECUADOR. *La Plata Island*, February 10, 1934, 24 specimens, 7–10 fms., AHF Sta. No. 213–34.

Geographic range. Southern California to Ecuador.

Remarks. It is difficult to tell this species from the others which have been described and the writer believes that all of the species in the genus will have to be critically examined and the genus revised before the validity of any can be satisfactorily established. The number of articles comprising the branches of the uropods, the number of articles of the antennae, the structure of the mature male gnathopod are features subject to some developmental variation but these characteristics are the primary features separating *P. pedispinis* from the other known species at this time.

Genus SYNAPSEUDES Miller

Synapseudes Miller, 1940, p. 311.
Type species. Synapseudes minutus Miller, 1940, pp. 311–313, fig. 6.

Diagnosis. Pleon consisting of three somites including the telson. Adults without pleopods. Gnathopods and second peraeopods lack epipods. Second antenna without a scale. Mandibular palp triarticulate. Dactyl of second peraeopod with a simple, pointed apex. Somites of pleon all of similar width. Facets present but eyelobes not separated from the cephalon.

Remarks. All species known from the area under consideration have spines on the inner margin of the first peduncular article of the first antenna.

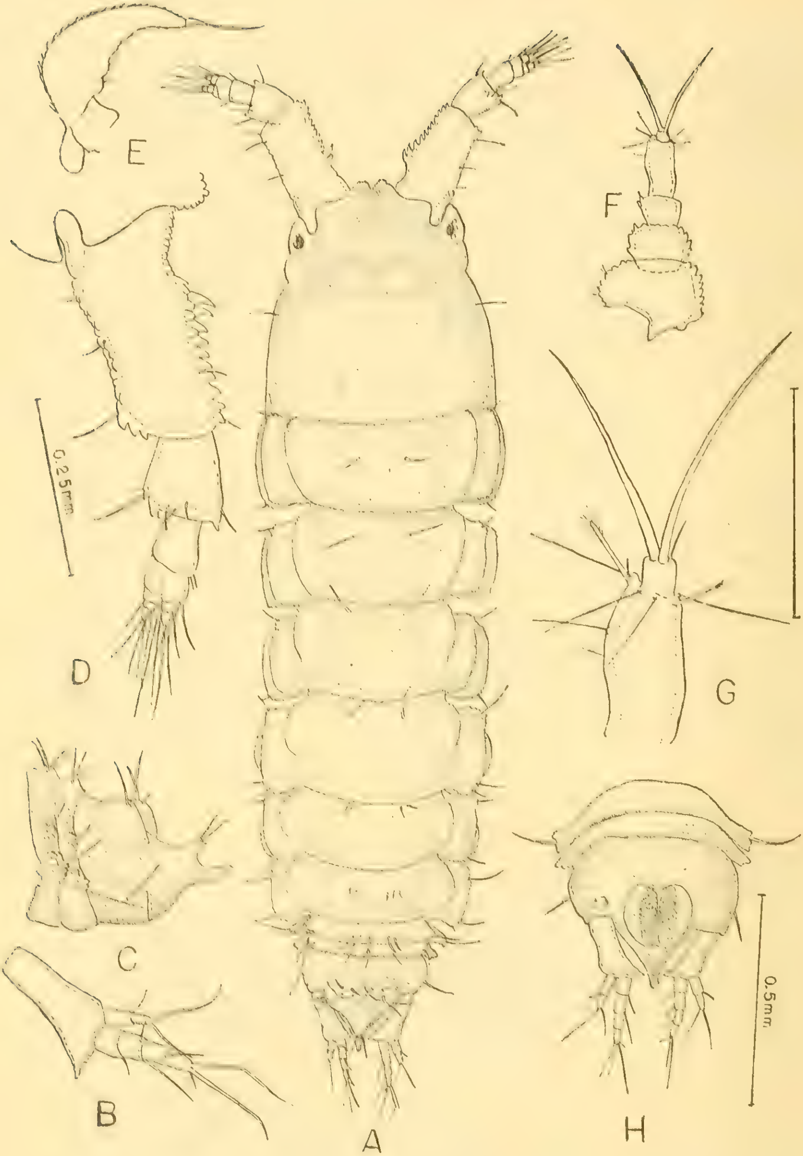
E
F
0.25mm
0.25 mm
D
G
C
0.5mm.
B
A
H

Fig. 10. *Synapseudes intumescens* Menzies, A. toto, B. uropod, C. lateral view of telson, D. first antenna, E. branchial gill of maxilliped, F. second antenna, G. apex of second antenna, H. ventral view of telson. Figures with similar magnification, A; B, D, F; C, H; G, E.

Key to the Species of Synapseudes

1. Second antenna with six articles. Endopod of uropod with three articles.
    B. Dactyl of medium sized male gnathopod with three teeth on inferior margin (Fig. 12C). . . . .*rudis* n. sp.
    B¹. Dactyl of medium sized male gnathopod with four teeth on inferior margin (Fig. 14D). . . . .*hancocki* n. sp.
A¹. Second antenna with five articles. Endopod of uropod with four articles.
    B. Telson lacks elevated swellings on dorsal surface. . . . . .*dispina* n. sp.
    B¹. Telson with elevated swellings on dorsal surface. . *intumescens* Menzies

SYNAPSEUDES INTUMESCENS Menzies

Figure 10

Synapseudes intumescens Menzies, 1949, pp. 509–515, figs. 41–42.

Diagnosis. Rostrum bifurcated. Second antenna with five articles. Endopod of uropod with four articles, exopod with two. Telson with an acutely pointed apex, above which is a narrow, cone-shaped, setiferous papilla; lateral and anterior to the cone-shaped papilla are two widely conical papillae.

Measurements. Holotype female, length 2.0 mm., width 0.4 mm. Allotype male length 1.6 mm., width 0.4 mm. (Menzies, 1949, p. 510).

Type locality. Marin County, California (Menzies 1949, p. 514).

Location of type. U. S. National Museum, Washington, D. C., Cat. No. 87416.

Material examined. CALIFORNIA. *Point Fermin*, San Pedro, October 21, 1949, 1 male, in kelp hold-fast, R. J. Menzies. *Willows Anchorage*, Santa Cruz Island, December 30, 1948, 7 specimens, AHF Sta. No. 1664–48.

MEXICO. *Guadalupe Island*, Melpomene Cove and 2¼ mi. N. of South Bluff, December 17–19, 1949, 44 specimens intertidal to 36 fms., AHF Sta. Nos. 1912–49, 1915–49, 1919–49, 1923–49.

Geographic range. Marin County, California to Guadalupe Island, Mexico.

Remarks. The above specimens extend the range of the species from Monterey Bay, California southward to Guadalupe Island, Mexico. Intertidal specimens were collected by washing rocks and algae with dilute formalin-seawater. Ovigerous specimens were found in December at Guadalupe Island, Mexico.

SYNAPSEUDES RUDIS new species

Figures 11–12

Diagnosis. Rostrum bifurcated. Second antenna with six articles. Endopod of uropod with three articles, exopod with two. Dorsum of telson lacking elevated swellings. Dactyl of medium sized male gnathopod with three teeth on inferior margin, excluding the apical claw as a tooth. Dactyl of large male gnathopod with an apical claw. Posterior border of lateral plate of cephalon separated from posterior border of gnathopodal sclerite by a short distance (Fig. 11 D); two tubercles present along inner margin between the borders.

Measurements. Holotype male, length 1.4 mm., width 0.3 mm. Allotype length 1.25 mm., width 0.25 mm.

Type locality. Melpomene Cove, Guadalupe Island, Mexico, December 18, 1949, holotype, allotype, and 11 paratypes, intertidal, AHF Sta. No. 1915–49.

Location of types. The types are deposited in the collections of the Allan Hancock Foundation, Cat. No. 4913, 4913a.

Material examined (exclusive of types). CALIFORNIA. *Santa Catalina Island,* White Cove, July 18, 1941, 3 specimens, AHF Sta. No. 1367–41; July 20, 1941, 2 specimens, AHF Sta. No. 1370–41; August 4, 1941, 5 specimens, AHF Sta. No. 1378–41, specimens from holdfasts of the kelps *Macrocystis* and *Eisenia.*

MEXICO. West Coast of Lower California, *E. San Benito Island,* April 26, 1950, 1 specimen, AHF Sta. No. 1946–50. *Entrada Point,* Magdalena Bay, May 2, 1950, 9 specimens, AHF Sta. No. 1961–50. Guadalupe Island, *Melpomene Cove* and 2¼ mi. N. of *South Bluff,* December 17, 19, 1949, 47 specimens, AHF Sta. Nos. 1912–49, 1919–49 and 1923–49.

Geographic range. Santa Catalina Island, California, to Guadalupe Island and Magdalena Bay, Lower California, Mexico.

Remarks. This species differs from *S. intumescens* and *S. dispina* in having a greater number of articles comprising the second antenna and in having a fewer number of articles comprising the uropodal endopod.

Most of the specimens were collected from kelp holdfasts in the intertidal zone. At Guadalupe Island specimens were taken from formalin-seawater washings of rocks encrusted with corals and bryozoa.

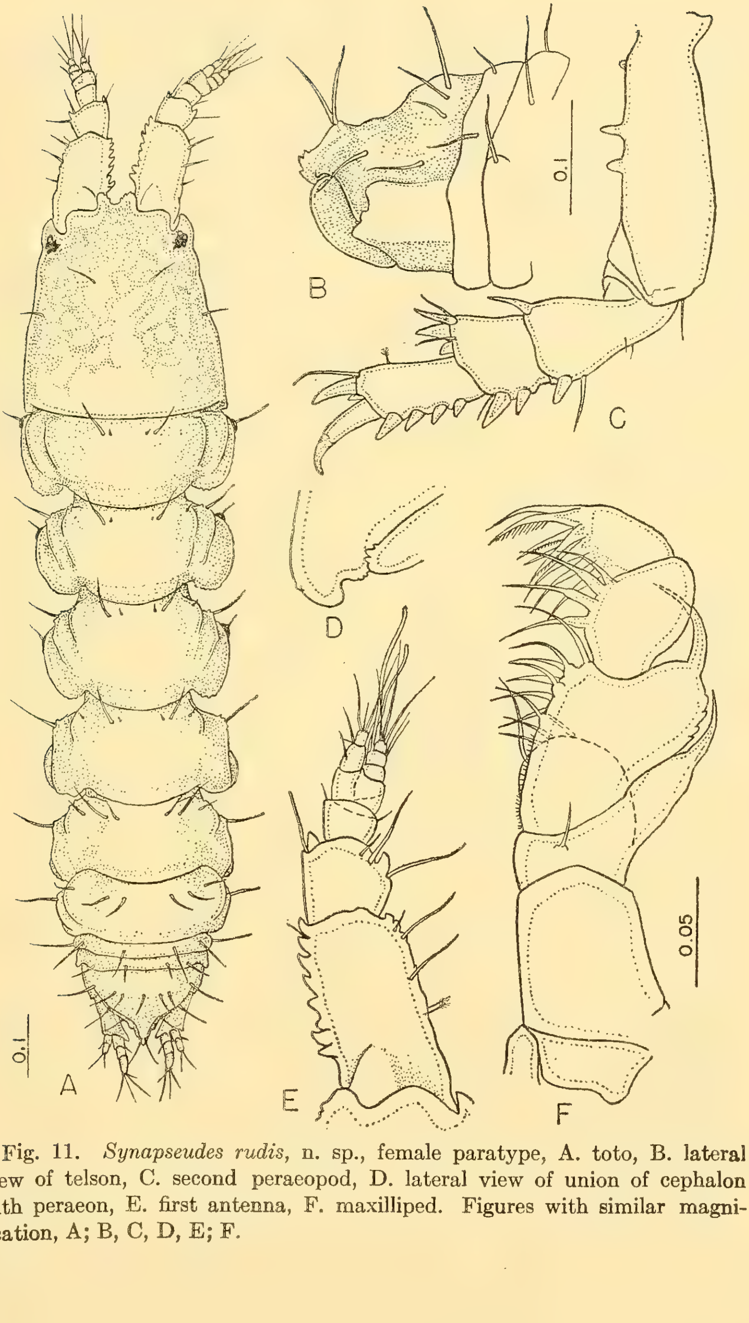

Fig. 11. *Synapseudes rudis,* n. sp., female paratype, A. toto, B. lateral view of telson, C. second peraeopod, D. lateral view of union of cephalon with peraeon, E. first antenna, F. maxilliped. Figures with similar magnification, A; B, C, D, E; F.

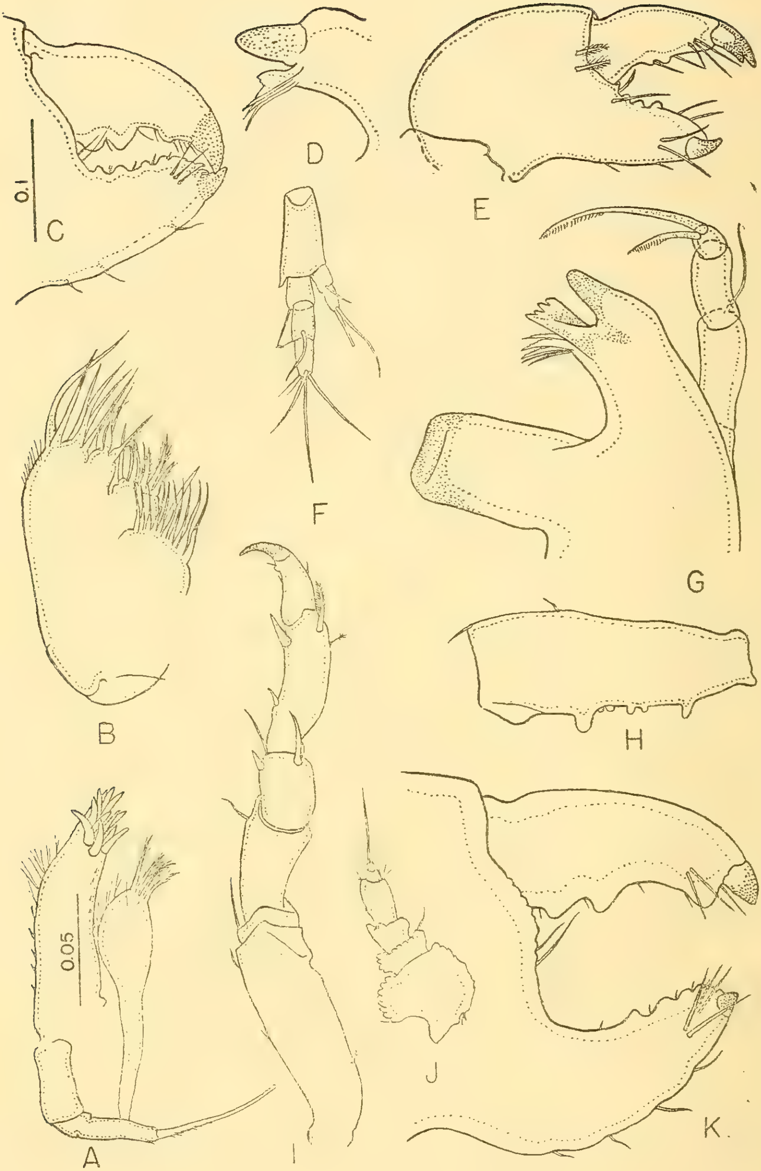

Fig. 12. *Synapseudes rudis*, n. sp., A. first maxilla, B. second maxilla, C. male first gnathopod, D. incisor and setal row of right mandible, E. female gnathopod, F. uropod, G. left mandible, H. basis of second peraeopod of female, I. seventh peraeopod, J. second antenna, K. gnathopod of mature male. Figures with similar magnification, A, B, D, G; C, E, F, H, I, J, K.

SYNAPSEUDES DISPINA new species

Figure 13

Diagnosis. Rostrum bifurcated. Second antenna with five articles. Endopod of uropod with four articles, exopod with two. Dorsum of telson lacking elevated swellings.

Measurements. Holotype female, length 2.0 mm., width 0.3 mm.

Type locality. Asunción Point, Lower California, Mexico, April 28, 1950, 1 female holotype, intertidal, AHF Sta. No. 1950–50. E. San Benito Island, Lower California, Mexico, April 26, 1950, 1 male paratype, intertidal, AHF Sta. No. 1946–50.

Location of types. The types are deposited in the collections of the Allan Hancock Foundation, Cat. No. 506.

Material examined. Types only.

Geographic range. Western coast of Lower California, Mexico, from E. San Benito Island to Asunción Point.

Remarks. This species differs from *S. intumescens* Menzies in lacking elevated papillae on the dorsum of the telson. It differs from *S. heterocheles* (Vanhöffen) because the exopod of the uropod consists of two and not one article and the endopod has four and not three articles. The second antenna figured by Vanhöffen (1914, p. 464, fig. 4) has at least six articles but Vanhöffen states that, "die unteren Antennen sind kurz, dreigliedrig . . ." In either case the second antenna of *S. dispina* differs from that of *S. heterocheles* because it consists of five articles.

It is conceivable that this species is a geographic variant of *S. intumescens* but without further material it is impossible for one to tell one way or the other.

SYNAPSEUDES HANCOCKI new species

Figure 14

Diagnosis. Rostrum bifurcated. Second antenna with six articles. Endopod of uropods with three articles, exopod with two. Dorsum of telson lacking elevated swellings. Dactyl of medium sized male gnathopod with four teeth, excluding apical claw as a tooth. Dactyl of large male gnathopod without an apical claw. Posterior border of lateral plate of cephalon separated from posterior border of gnathopodal sclerite by a considerable distance (Fig. 14G); about six tubercles present along inner margin between the borders.

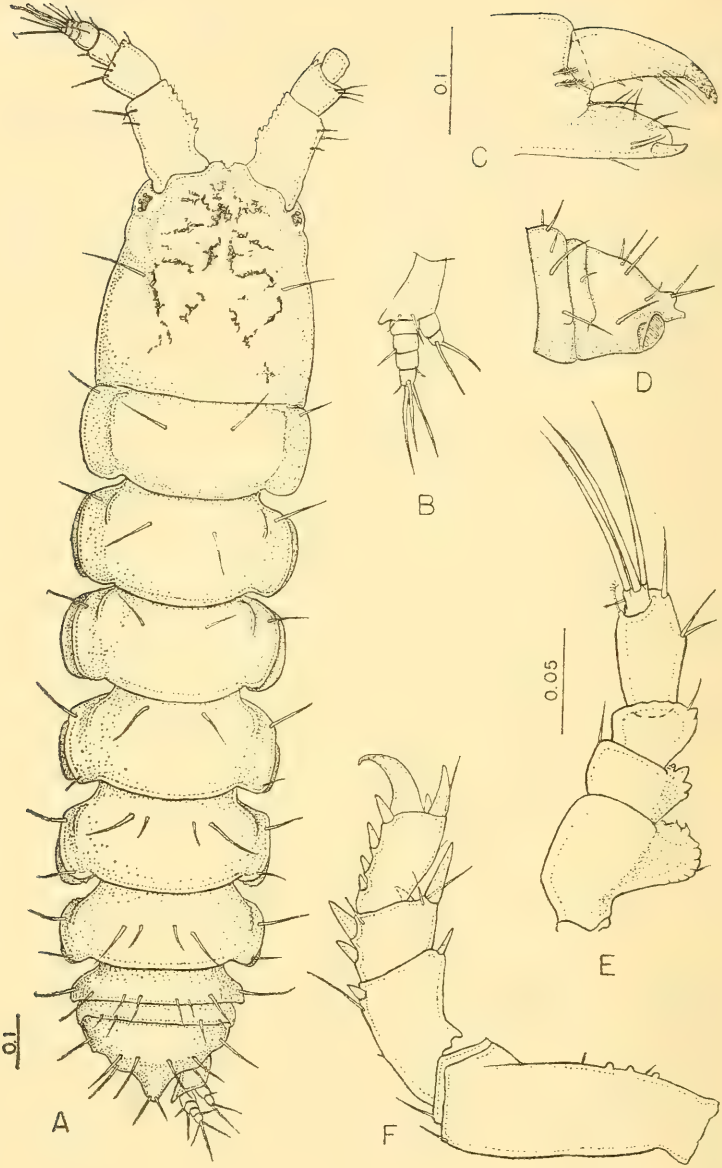

Fig. 13. *Synapseudes dispina*, n. sp., A. toto, B. uropod, C. female gnathopod, D. lateral view of telson, E. second antenna, F. second peraeopod. Figures with similar magnification, A, D; B, C, F; E.

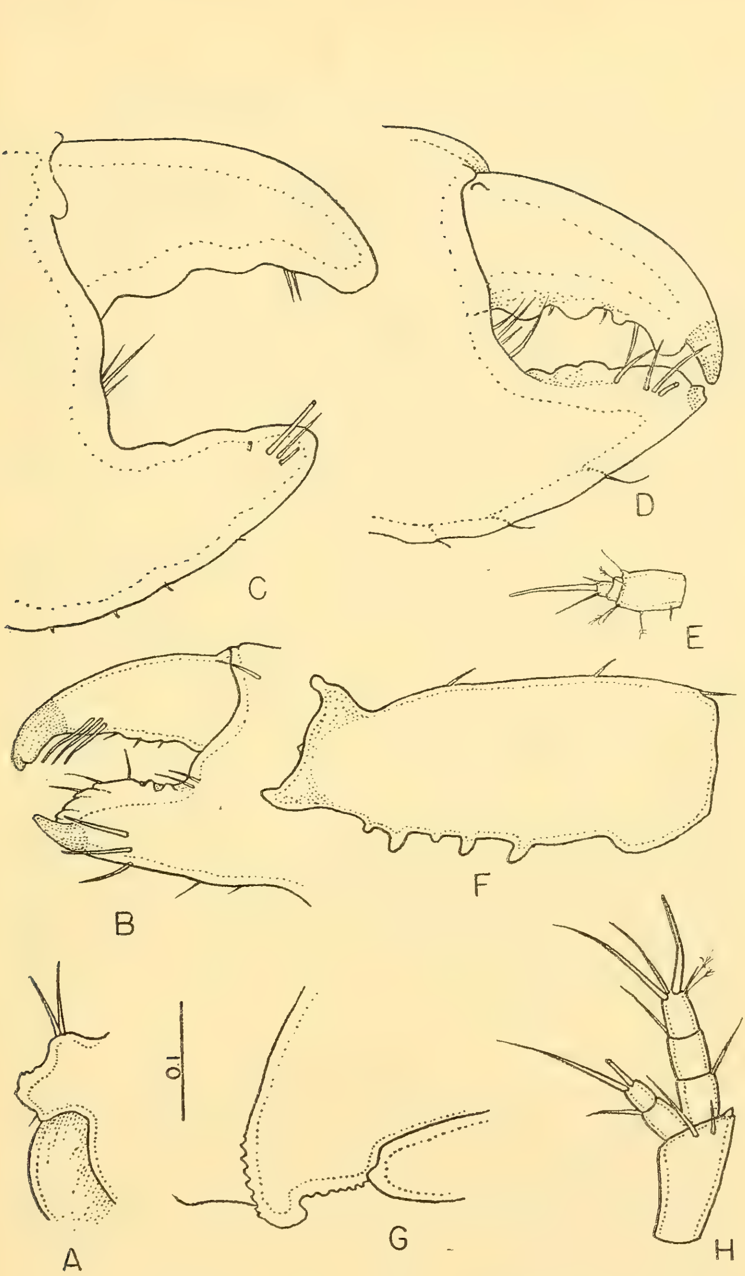

Fig. 14. *Synapseudes hancocki*, n. sp., A. lateral view of apex of telson, B. female gnathopod, C. male gnathopod, D. male gnathopod, E. distal articles of second antenna, F. basis of second peraeopod of female, G. lateral view of cephalic-first peraeonal somitic union, H. uropod. Figures with similar magnification, A, B, C, D, E, G, H; F not known.

Measurements. Holotype male, length 1.8 mm., width 0.3 mm. Ovigerous female allotype, length 1.9 mm., width 0.3 mm.

Type locality. Lobos de Afuera Island, Peru, January 17, 1935, holotype, allotype, and 29 paratypes, intertidal zone, AHF Sta. No. 391–35.

Location of types. The holotype, allotype, and 19 paratypes are deposited in the collections of the U. S. National Museum, Washington, D. C. Ten paratypes are in the collections of the Allan Hancock Foundation.

Material examined (exclusive of types). Tagus Cove, Albemarle Island, Galapagos Islands, January 14, 1934, 1 female, from coral, AHF Sta. No. 152–34.

Geographic range. Galapagos Islands and Peru.

Remarks. The differences which are enumerated in the diagnoses between *S. hancocki* and *S. rudis* seem very slight. They are not differences of sex or age of the specimens and are consistent in the material examined and, therefore, indicate the probability of the distinctness of the species.

Genus PAGURAPSEUDES Whitelegge

Pagurapseudes Whitelegge, 1901, pp. 209–210.

Pagurotanais Bouvier, 1918, pp. 12–15.

Type species. Pagurapseudes spinipes Whitelegge, 1901, pp. 210–215, figs. 16a-h.

Diagnosis. Pleon consisting of six somites including the telson. Adult with zero to three pairs of pleopods. Gnathopod and second peraeopod with an epipod. Second antenna without a scale. Mandibular palp triarticulate. Dactyl of second peraeopod with a simple, pointed apex. Somites of pleon all of similar width. Facet bearing separated eyelobes present.

Remarks. This genus appears to contain two species, *P. spinipes* and *P. bouryi* (Bouvier, *vide* Lang, 1949, p. 4). *P. heterocheles* Vanhöffen has been referred to *Synapseudes* (Menzies, 1949, p. 510).

Pagurapseudes has a coiled abdomen and its members occupy small univalve shells much like the pagurid crabs. This characteristic habit was noted earlier by Whitelegge and Bouvier. Lang's (1949, p. 4) statement that *Pagurapseudes* is "commensal among the Pagurides," is possibly a misinterpretation of Whitelegge's observation that, "It is distinctly paguroid in habit, living in small univalve shells and in company with young hermit crabs."

PAGURAPSEUDES LAEVIS new species

Figures 15–16

Diagnosis. Rostrum triangulate, directed downward, apex sharp. Frontal margin between rostrum and eye with a median tooth. Epipod of gnathopod and second peraeopod with only one article. Frontal margin of ventral surface of eye with cuboidal teeth. Second article of second antenna equals the length of third article. Male with one pair of pleopods; female without pleopods. Tips of gnathopods golden in color.

Measurements. Holotype male, length, 2.5 mm., width 0.4 mm. Allotype lacking oostegites, length 2.5 mm., width 0.4 mm.

Type locality. California, one mi. NW of White Cove, Santa Catalina Island, August 4, 1941, holotype, allotype, and one male paratype, AHF Sta. No. 1378–41.

Location of types. The types are deposited in the collections of the Allan Hancock Foundation, Cat. No. 413, 413a.

Material examined (exclusive of types). Mexico, Guadalupe Island, Melpomene Cove, December 19, 1949, 3 specimens, 50–51 fms., AHF Sta. No. 1920–49.

Geographic range. Santa Catalina Island to Guadalupe Island, Mexico.

Remarks. This species differs from *P. spinipes* in having a triangulate and not a truncate rostrum, and in having uniarticulate and not biarticulate epipods. In these respects it resembles *P. bouryi* (Bouvier). It differs from the latter in having a more acute rostrum and a second antenna with six articles. In *P. bouryi* the rostrum is wide near its apex and the second antenna has only five articles (Bouvier, 1918, figs. 5, 7).

Genus KALLIAPSEUDES Stebbing

Kalliapseudes Stebbing, 1910, pp. 86–87.
Type species. Kalliapseudes makrothrix Stebbing, 1910, pp. 86–88.

Diagnosis. Pleon consisting of six somites including the telson. Adult with five pairs of pleopods. Gnathopod and second peraeopod with or without an epipod. Second antenna with a scale. Mandibular palp with one or two articles. Dactyl of second peraepod with a blunt, setiferous apex.

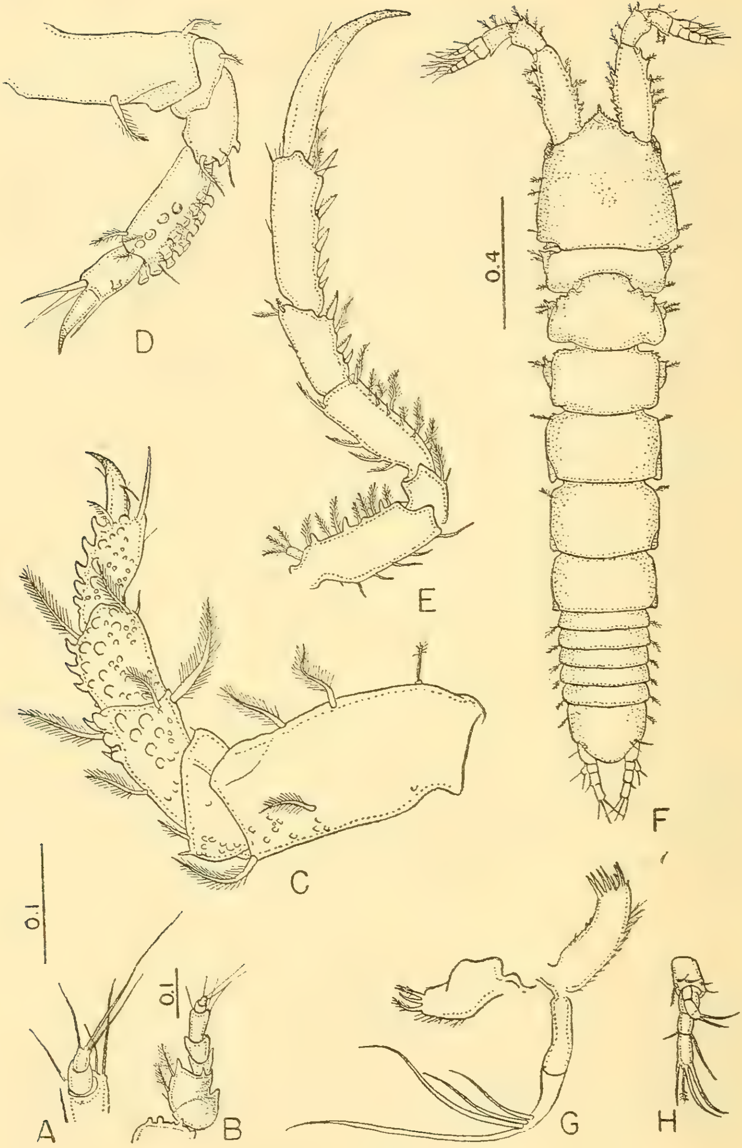

Fig. 15. *Pagurapseudes laevis*, n. sp., A. distal articles of second antenna, B. second antenna, C. third peraeopod, D. seventh peraeopod, E. second peraeopod, F. toto, G. first maxilla, H. uropod. Figures with similar magnification, A, C, D, G; B, E, H; F.

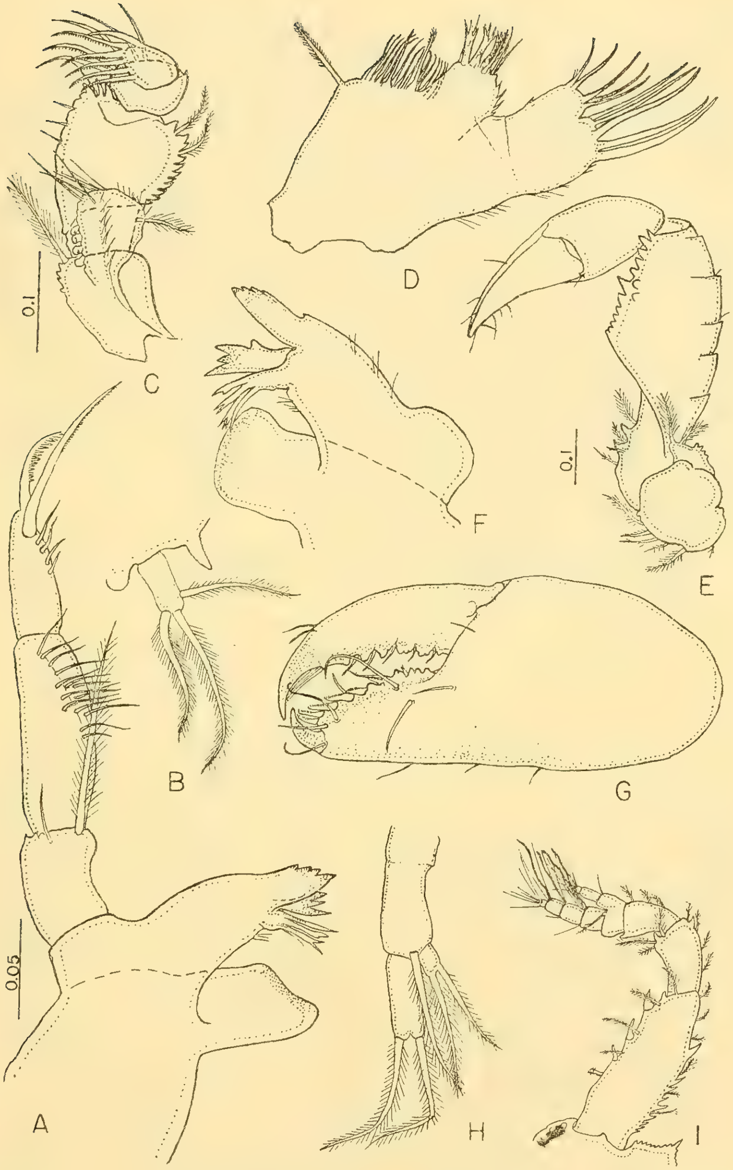

Fig. 16. *Pagurapseudes laevis*, n. sp., A. left mandible, B. epipod of second peraeopod, C. maxilliped, D. second maxilla, E. gnathopod, F. left mandible, G. gnathopod, H. first pleopod, I. first antenna, eye, and rostrum. Figures with similar magnification, A, B, D, F, H; C, G; E, I.

Remarks. This genus is known to contain, in addition to those described herein as new, at least four species, *K. makrothrix* Stebbing (1910), *K. obtusifrons* (Haswell, 1881), *K. primitivus* Nierstrasz (1913), and *K. mauritanicus* Monod (1923). Lang (1949, p. 3) states, "to me it appears to be most probable that *makrothrix* and *primitivus* are identical with *obtusifrons*. The systematics within the genus can only be cleared up, however, by means of ocular inspection of all the species." This latter remark seems very reasonable and indicates the difficult situation in which the systematics of the Tanaidacea are today. On the other hand, the fact that the mandibular palp of *K. makrothrix* is figured as having a short apical article, whereas, Nierstrasz indicates no short apical article on the mandibular palp of *K. primitivus*, is an indication to me that *primitivus* and *makrothrix* are more probably different than identical.

Key to the Species of Kalliapseudes

A. Rostrum pointed. Body largely devoid of pigment, white. . *crassus* n. sp.
A¹. Rostrum blunt. Body green in color. . . . . *viridis* n. sp.

KALLIAPSEUDES CRASSUS new species

Figures 17–20

Diagnosis (adult female). Eyes and eyelobes present. Outer branch of first antenna with nine articles, inner with three. Second antenna with eleven articles. Mandibular palp uniarticulate, united along its outer margin with the mandible. Exopod of uropod with three articles, endopod with about eighteen articles. Maxilliped with two coupling hooks. Dactyl of seventh peraeopod apically bifid. Rostrum pointed. Telson with about twenty-two setae on posterior margin. Body with little pigment, white in color. Immovable finger of gnathopod exceeds two-thirds the length of the dactyl.

Measurements. Holotype female, length 8.0 mm., width 1.0 mm.

Type locality. San Quintin Bay, west coast of Lower California, Mexico, April 6–7, 1950, 34 specimens, ovigerous females and young, collected by Charles Horvath, Donald Reish, and R. J. Menzies.

Location of types. The types are deposited in the collections of the Allan Hancock Foundation. Some paratypes have been sent to Dr. Karl Lang, Curator, Naturhistoriska Riksmuseum, Stockholm, Sweden.

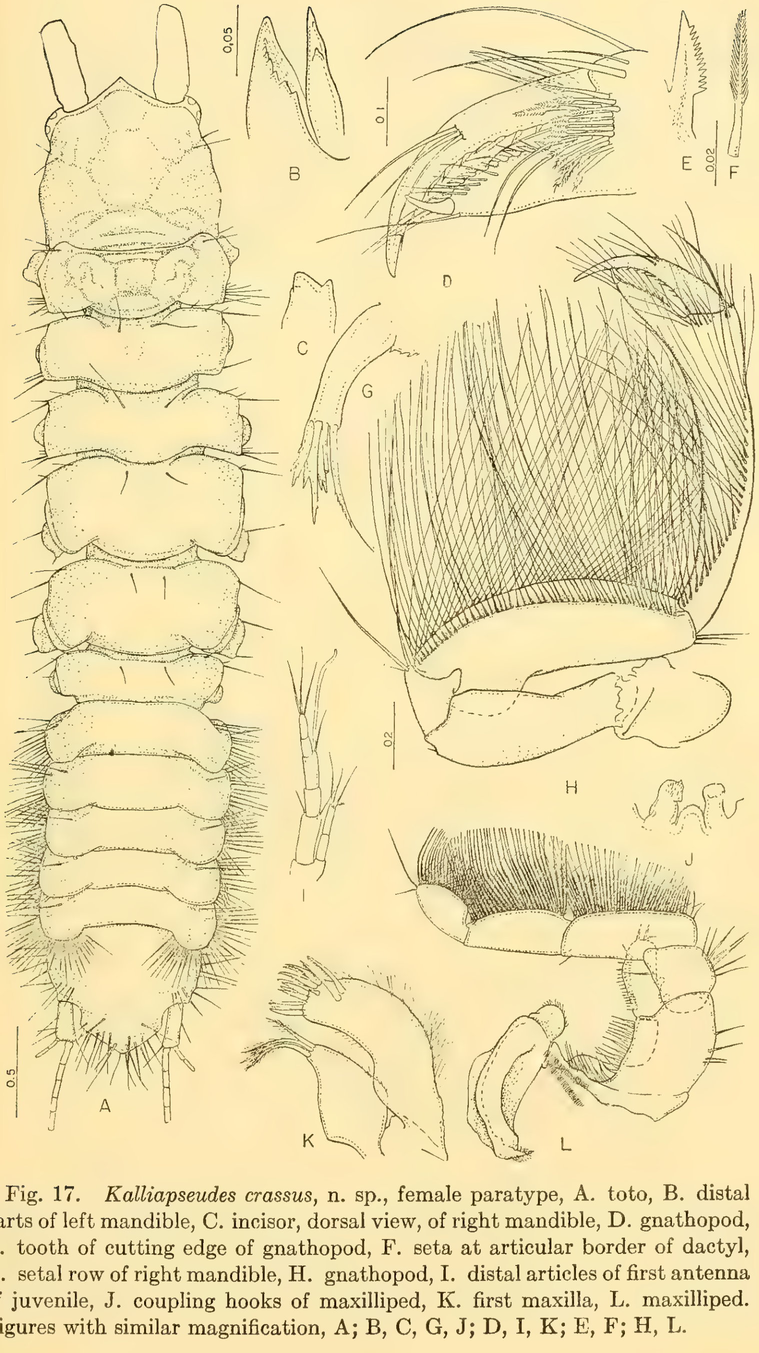

Fig. 17. *Kalliapseudes crassus*, n. sp., female paratype, A. toto, B. distal parts of left mandible, C. incisor, dorsal view, of right mandible, D. gnathopod, E. tooth of cutting edge of gnathopod, F. seta at articular border of dactyl, G. setal row of right mandible, H. gnathopod, I. distal articles of first antenna of juvenile, J. coupling hooks of maxilliped, K. first maxilla, L. maxilliped. Figures with similar magnification, A; B, C, G, J; D, I, K; E, F; H, L.

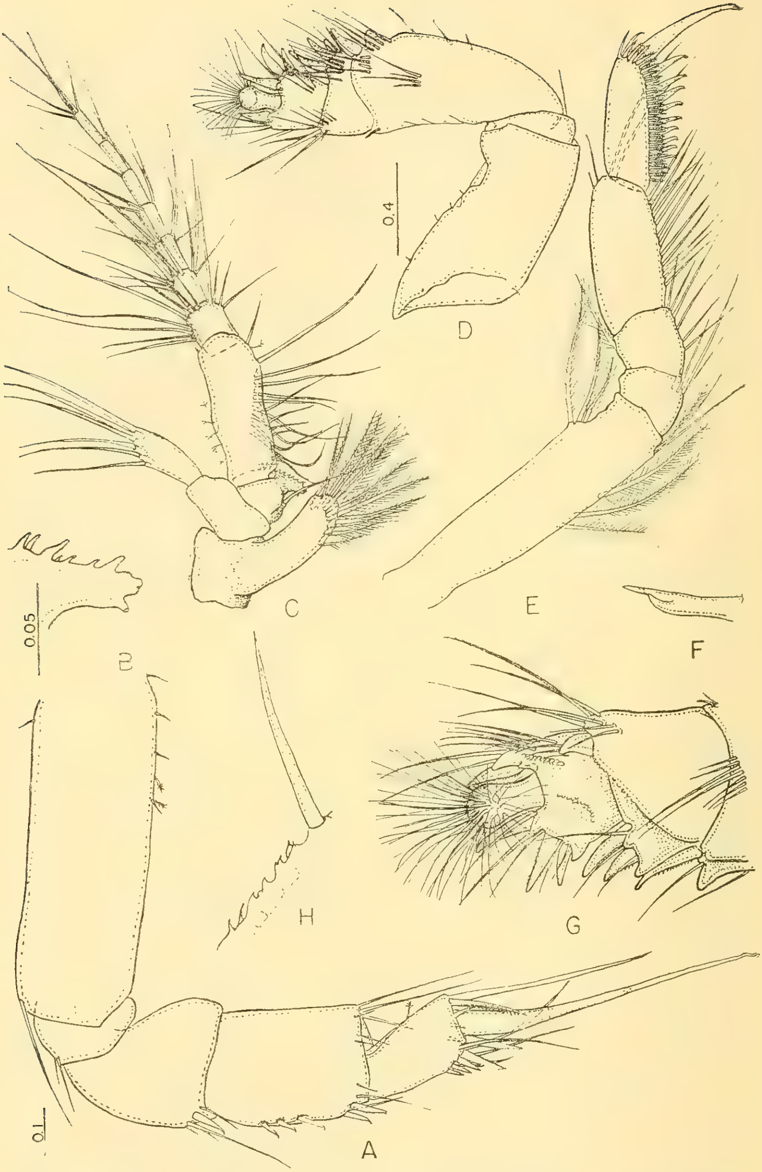

Fig. 78. *Kalliapseudes crassus*, n. sp., female, paratype, A. third peraeopod, B. superior margin of third article of second antenna, C. second antenna, D. second peraeopod, E. seventh peraeopod, F. apex of dactyl of seventh peraeopod G. distal articles of second peraeopod, H. spinulate edge of peduncle of first antenna. Figures with similar magnification, A, C, E, G; B, F, H; D.

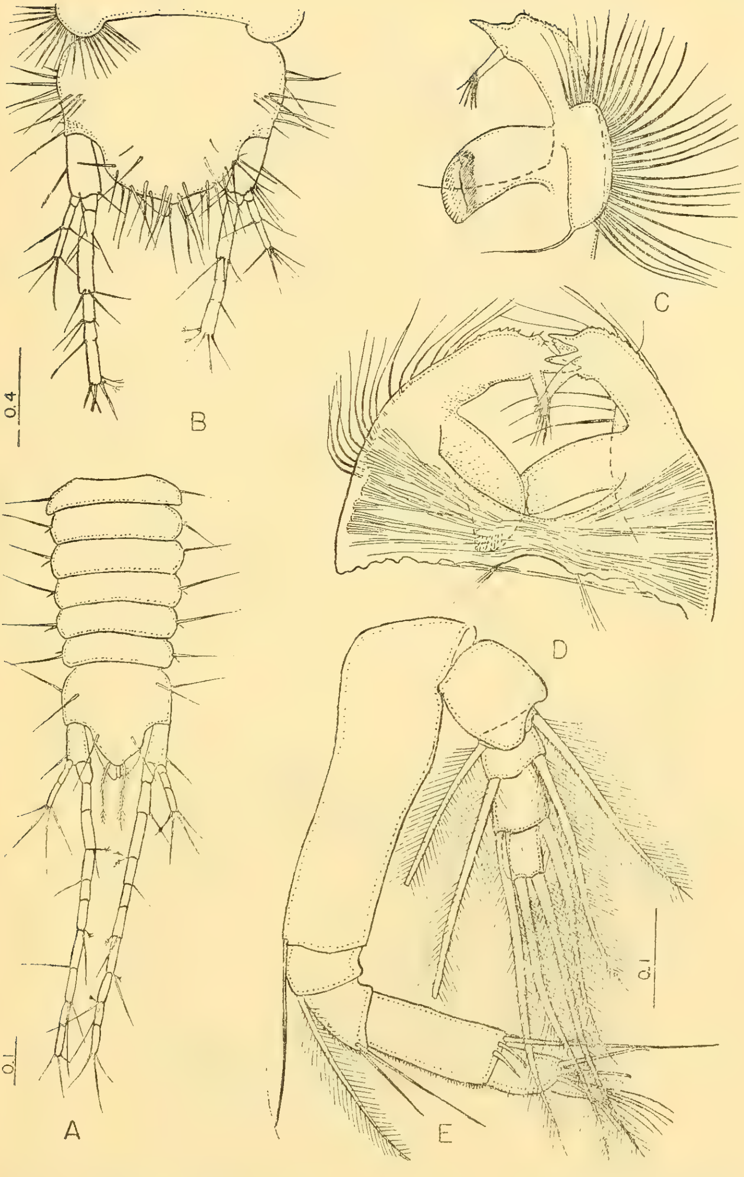

Fig. 19. *Kalliapseudes crassus*, n. sp., paratype. A. last peraeonal somite, pleon and uropods of juvenile removed from marsupial pouch, B. adult telson, C. palpar surface of right mandible, D. mandibles showing how they are fused together on midline, E. fifth peraeopod with exopod, of juvenile removed from marsupial pouch. Figures with similar magnification, A, C, D; B; E.

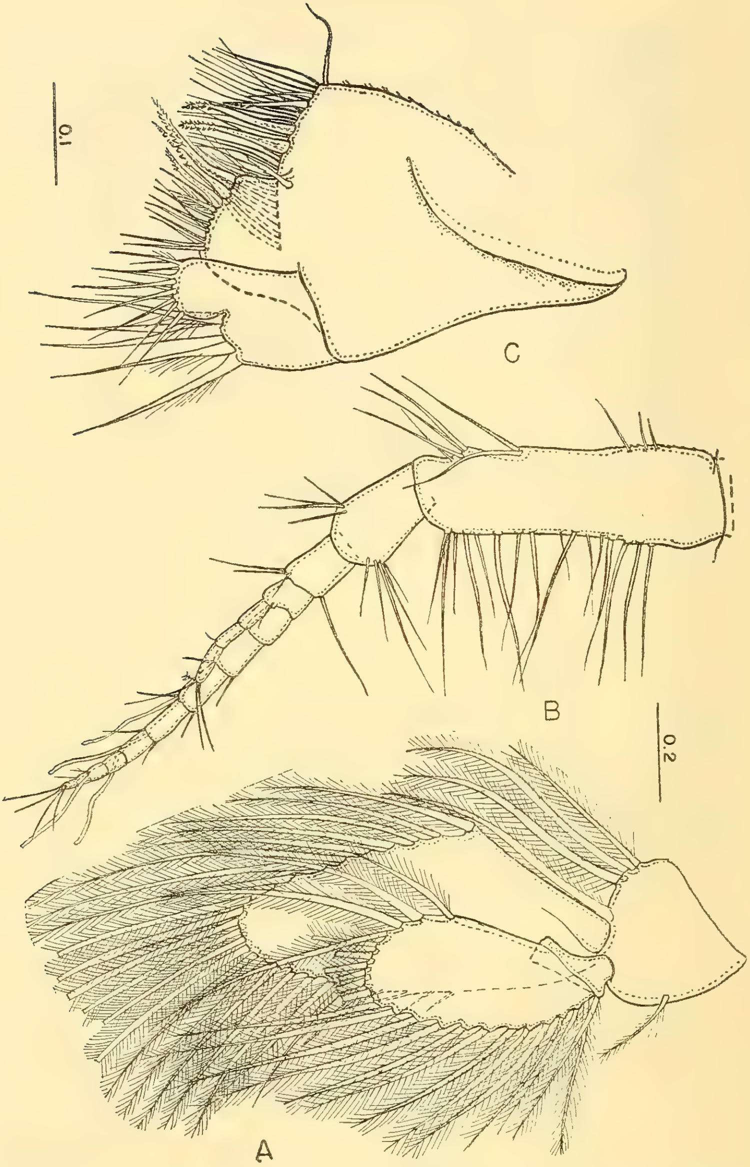

Fig. 20. *Kalliapseudes crassus*, n. sp., female paratype, A. first pleopod, B. first antenna, C. second maxilla. A–B with similar magnification.

Specimens examined. Types only.

Geographic range. Known only from the type locality.

Remarks. I concur with Lang (1949, p. 3) that "die Lade" of Nierstrasz (1913, pl. II) is the molar process. The mandibles are not as other writers have figured them, at least in this species. Both the right and left mandibles are united by a sclerotized band near their bases. The setal row is similar to what Stebbing (1910) describes for *K. makrothrix,* being located at the apex of an elongated, tubular projection of the mandibles. The lacinia is present only on the left mandible.

Of particlar interest in this species are the changes which the young exhibit in metamorphosis. The young which have recently emerged from the marsupium are markedly different from the adults. There is no doubt that they belong to the same species because they are identical in all respects with specimens removed from the marsupium. In contrast to the adult they have no pleopods and very few setae are present on the lateral margins of the somites of the pleon. In addition they possess a structure not found on adults, namely, the fifth and sixth peraeopods have relatively large pentarticulate "exopods" attached to the proximal end of the elongate basis. As the animal gets larger, the endopod of the uropod increases in number of articles from ten to about eighteen, but the number of articles comprising the exopod remains at three. The outer branch of the first antenna adds four articles during the metamorphosis while the inner branch adds but two.

The arrangement of double rows of plumose setae on the articles of the gnathopod, maxilliped, and mandibular palp suggests that *Kalliapseudes* is a filter-feeder. A similar situation prevails in the other species of the genus. The specimens reported here were taken from a mud-sand substrate among sponges.

This species differs from the others belonging to the genus in having faintly separated eyelobes which bear facets. It differs from *K. obtusifrons* in having the apex of the telson somewhat pointed and not bifid.

The eyes of *K. crassus* are on lobes but the lobes, as in the following species, do not appear to be entirely separated from the cephalon as they are in *Parapseudes,* for example, and only a faint line indicates their demarkation from the cephalon. No epipods were observed to be attached to the gnathopod and second peraeopod of this species.

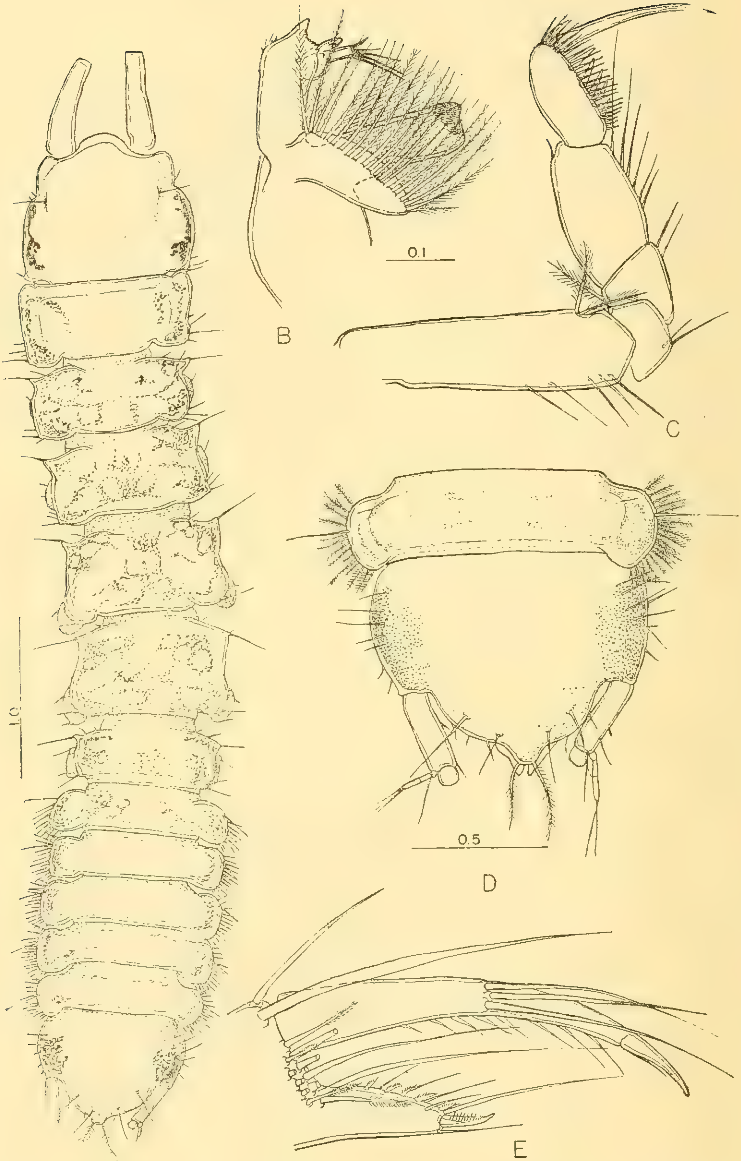

Fig. 21. *Kalliapseudes viridis*, n. sp., female paratype, A. toto, B. left mandible, C. seventh peraeopod, D. telson and fifth somite of pleon, E. female gnathopod. Figures with similar magnification, A; B, C, E; D.

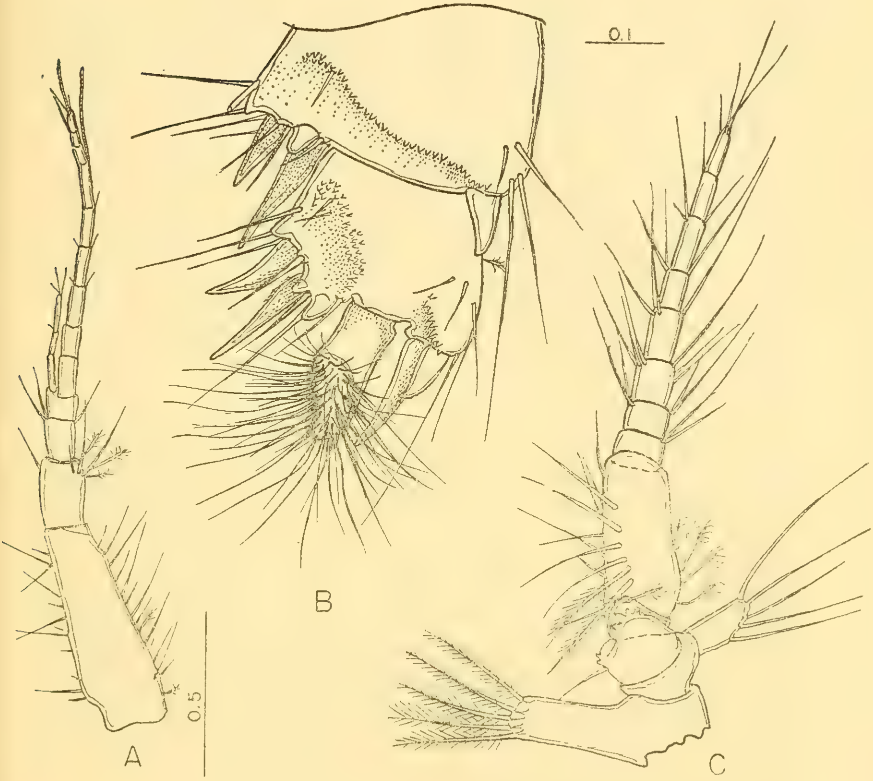

Fig. 22. *Kalliapseudes viridis*, n. sp., A. first antenna, B. apical articles second peraeopod, C. second antenna. Figures with similar magnification, A; B, C.

KALLIAPSEUDES VIRIDIS new species

Figures 21–22

Diagnosis. Eyelobes present, facets lacking. Outer branch of first antenna with nine articles, inner with three. Second antenna with twelve articles. Mandibular palp uniarticulate, united along part of its inner margin with the mandible. Exopod of uropod with three articles, endopod with twenty-five to twenty-six articles. Maxilliped with two coupling hooks. Dactyl of seventh peraeopod apically bifid. Rostrum blunt. Telson with eleven setae on posterior margin. Color green. Immovable finger of gnathopod less than one half as long as dactyl.

Measurements. Holotype, female, length 7.2 mm., width 1.0 mm. Allotype (immature male) length 5.0 mm., width 0.7 mm.

Type locality. South Bay, Cedros Island, Lower California, Mexico, April 19, 1951, holotype, allotype, and one female paratype, 16–19 fathoms, AHF Sta. No. 2026–51.

Location of types. The types are deposited in the collections of the Allan Hancock Foundation, Cat. No. 512, 512a.

Specimens examined. Types only.

Geographic range. Known only from the type locality.

Remarks. The maxillae, maxillipeds, and pleopods are so similar to those figured for *K. crassus* that they were not illustrated. This species differs from *K. crassus* in having a blunt rostrum, in being green in color, in having eyelobes which lack facets, and in having the immovable finger of the gnathopod exceptionally short. No epipods were observed.

This species differs from *K. makrothrix* Stebbing (1910) in having a uniarticulate mandibular palp, and from *A. primitivus* Nierstrasz (1913) in having a blunt rostrum. It differs from *K. mauritanicus* Monod(1923) in having only the first article of the uropodal exopod short and not both the first and second short and subequal as in *K. mauritanicus*. Unlike *K. obtusifrons* the telson has a median posterior lobe and is not bifid.

Genus IMITAPSEUDES new genus

Type species. Imitapseudes glebosus n. sp.

Diagnosis. Pleon consisting of six somites including the telson. Adult with five pairs of pleopods. Gnathopod and second peraeopod without an epipod. Second antenna with a scale. Mandibular palp triarticulate. Dactyl of second peraeopod with a simple, pointed apex. First somite of pleon much narrower than other somites, lacking the lateral expansions which characterize the other pleonal somites. Telson with a "pseudosegment" on lateral margin near anterior end.

Here a structure similar to the lateral expansions characteristic of the last five pleonal somites is present, but there is no separation of a somite. Facet bearing separated eyelobes present.

Remarks. This genus differs from *Apseudes,* which it resembles considerably, in the lack of epipods and in the peculiar morphology of the pleon. Another possible difference is in the presence of parallel ridges and grooves on the inner surface of the carpal article of each mature male gnathopod. This structure bears an interesting resemblance to the stridulating ridges present on the appendages of other crustaceans. It functions, however, perhaps to act as a coupling apparatus holding the apposed carpal articles together rather than to act as a noise-making device.

Imitapseudes is close to *Apseudomorpha* Miller (1940, p. 315). Two species are known to belong to the latter genus, *A. oahuensis* Miller, the type species, and *A. avicularia* (Barnard) (Lang, 1949, p. 5). It is possible that *Apseudes hirsutus* Stebbing should also be referred to *Apseudomorpha.* Lang (in letter) has discovered that the peduncle of the uropods of *Apseudomorpha* consists of only one article and this makes the similarity between the two more striking. The structure of the telson of *A. avicularia* is similar to that of several species of *Imitapseudes.* The pleonal structure is, however, markedly different; all somites except the fifth of *A. avicularia* being similar to *Imitapseudes.* The reverse is true in *A. oahuensis,* where the pleon is similar to *Imitapseudes* but where the telson is very different. At least one good characteristic separates the two genera, in *Apseudomorpha* only one pair of pleopods occur, whereas, in *Imitapseudes* there are five pairs. Separated eyelobes were neither mentioned nor figured for the two species of *Apseudomorpha* but their existence should not be ruled out until the specimens are re-examined (Lang, 1949, p. 4).

It is possible that *Apseudes timaruvia* Chilton (1882, p. 148) might belong to either *Apseudomorpha* or *Imitapseudes.* The species will, however, have to be redescribed before a positive generic assignment can be made, as its characteristics are too imperfectly known. Shiino's (1951) *Metapseudes albidus* no doubt belongs in *Imitapseudes* (see Addendum).

Key to the Species of Imitapseudes

A. First article of uropodal exopod one-half the length of second.
  B. Exopod of pleopod (both sexes) with two articles.................. .... *magdalenensis* n. sp.

B¹. Exopod present on pleopod of male only. This has one article...... .... *veleronis* n. sp.

A¹. First article of uropodal exopod two times the length of second......... .... *glebosus* n. sp.

IMITAPSEUDES GLEBOSUS new species

Figures 23–24

Diagnosis. Peduncle of first antenna with three articles; first with two large spines on upper edge of inner surface. Second antenna with seven to eight articles. Exopod of uropod with three articles; first article two times the length of the second; second as long as third. Pleopods of both sexes similar, consisting of an elongate peduncle with two uniarticulate branches.

Measurements. Mature male holotype, length 1.9 mm., width 0.32 mm. Allotype, ovigerous female, length 1.8 mm., width 0.4 mm.

Type locality. Melpomene Cove, Guadalupe Island, Mexico, December 17, 1949, holotype, allotype, and 161 paratypes, intertidal zone, under rocks and on algae, AHF Sta. No. 1912–49.

Location of types. The types are deposited in the collections of the Allan Hancock Foundation, Cat. No. 4912, 4912a.

Material examined (exclusive of types). CALIFORNIA. *Santa Barbara Island,* four mi. E. of landing, August 28, 1941, 1 ovigerous female, 40 fms., sand, AHF Sta. No. 1398–41. *Santa Catalina Island,* Farnsworth Bank, September 7, 1949, 1 male, 8 fms., AHF Sta. No. 1903–49.

MEXICO. Lower California, west coast. Six mi. SW of *San Carlos Point,* April 25, 1950, 1 ovig. female, 20 fms., rock, AHF Sta. No. 1944–50 Guadalupe Island, *Melpomene Cove,* December 1949, 52 specimens, AHF Sta. No. 1915–49 and 1923–49, with *Synapseudes rudis* and *Synapseudes intumescens.*

ECUADOR. *La Plata Island,* February 10, 1934, 2 females, 7–10 fms., AHF Sta. No. 213–34.

Geographic range. Channel Islands, California to Ecuador.

Remarks. The number of articles comprising the branches of the uropods was constant. In contrast, the number of articles comprising the branches of the flagellum of the first antenna increased as the size of the animal increased (Figure 24E-G). The elongate first article of the uropod distinguishes this species from *I. magdalenensis* and *I. veleronis.*

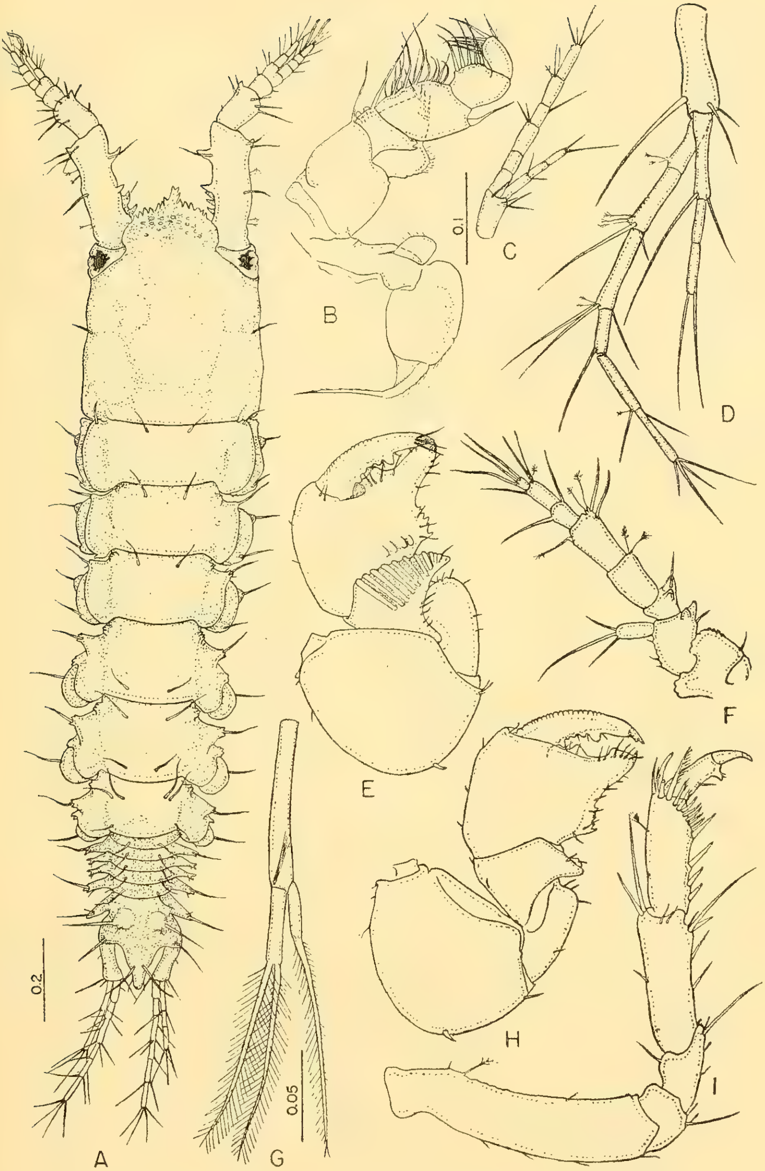

Fig. 23. *Imitapseudes glebosus*, n. sp., paratype, A. toto, B. maxilliped, C. uropod, D. uropod, E. inner surface of male gnathopod, F. second antenna, G. first pleopod, H. outer surface of male gnathopod, I. seventh peraeopod. Figures with similar magnification, A, E, H; B, C, D, F, I; G.

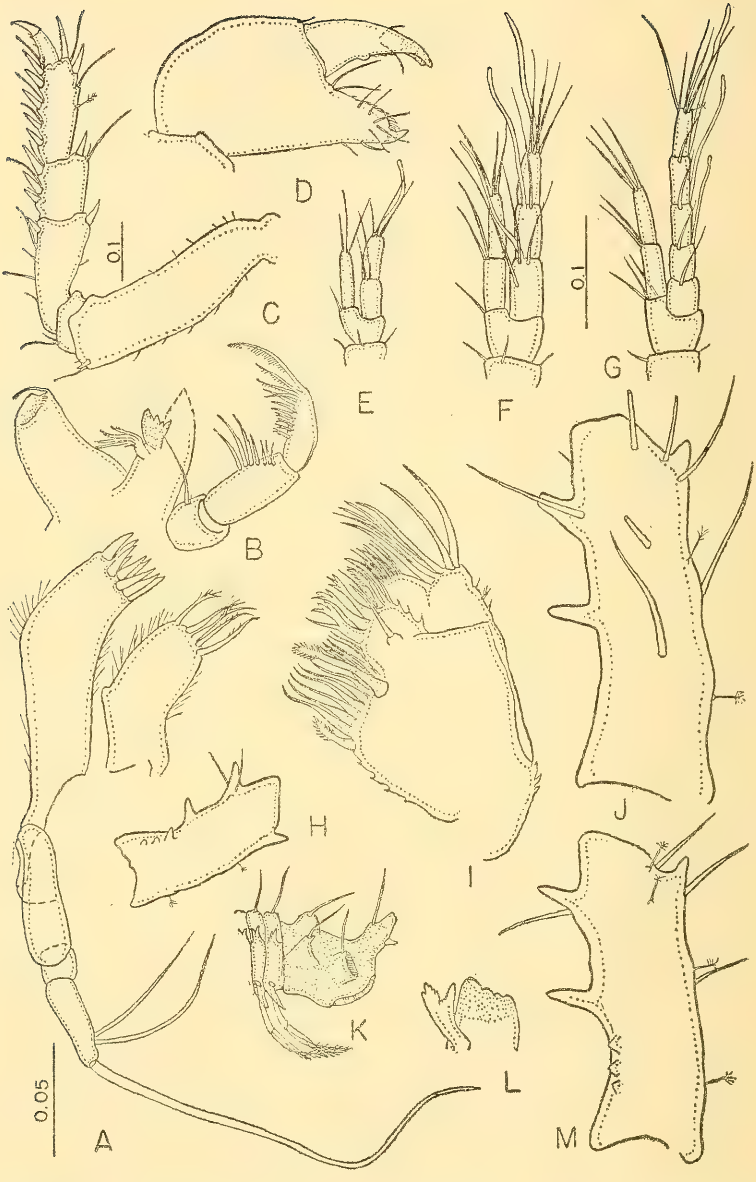

Fig. 24. *Imitapseudes glebosus*, n. sp., paratype, A. first maxilla, B. left mandible, C. second peraeopod, D. gnathopod of female, E–G. flagellar articles of first antenna, H, J, M. first peduncular article of first antenna, I. second maxilla, K. lateral view of telson, L. incisor and lacinioid seta of right mandible. Figures with similar magnification, A, B, I, L; C, K; D, E, F, G, H, J, M.

IMITAPSEUDES MAGDALENENSIS new species

Figure 25A–E

Diagnosis. Peduncle of first antenna with three articles; first article with four to five large spines on the upper edge of the inner surface. Second antenna with seven to eight articles. Exopod of uropod with three articles; first article one half the length of second; second shorter than third. Pleopods of both sexes similar, consisting of an elongate peduncle having a biarticulate exopod and an uniarticulate endopod.

Measurements. Mature male holotype, length, 2.0 mm., width 0.4 mm. Ovigerous allotype, length 2.0 mm., width 0.4 mm.

Type locality. Entrada Point, Magdalena Bay, Lower California, Mexico, May 2, 1950, holotype, allotype, and over 90 paratypes, intertidal, AHF Sta. No. 1961–50.

Location of types. The types are deposited in the collections of the Allan Hancock Foundation, Cat. No. 507, 507a.

Material examined (exclusive of types). MEXICO, Lower California, west coast, E. of *San Benito Island*, April 26, 1950, 12 specimens, shore, AHF Sta. No. 1946–50. W. side of middle *San Benito Island*, May 8, 1950, 1 ovig. female, shore, AHF Sta. No. 1976–50.

Geographic range. West coast of Lower California, Mexico, from San Benito Island to Magdalena Bay.

Remarks. This species is closely related to *I. velcronis*, from which it differs only in the structure of the pleopods.

IMITAPSEUDES VELERONIS new species

Figure 25F–G

Diagnosis. This species resembles *I. magdalenensis* so closely that the diagnosis for the latter applies to *I. veleronis* almost exactly. The two species differ, however, in one significant and consistent respect. The pleopods of the female of *I. veleronis* have only one branch, whereas those of the male have two very short uniarticulate branches.

Measurements. Male holotype, length 1.5 mm., width 0.25 mm. No allotype selected.

Type locality. Octavia Bay, Colombia, January 28, 1935, holotype male, 1 female paratype, shallow water, coral, AHF Sta. No. 435–35.

Location of type. The types are deposited in the collections of the U. S. National Museum, Washington, D. C.

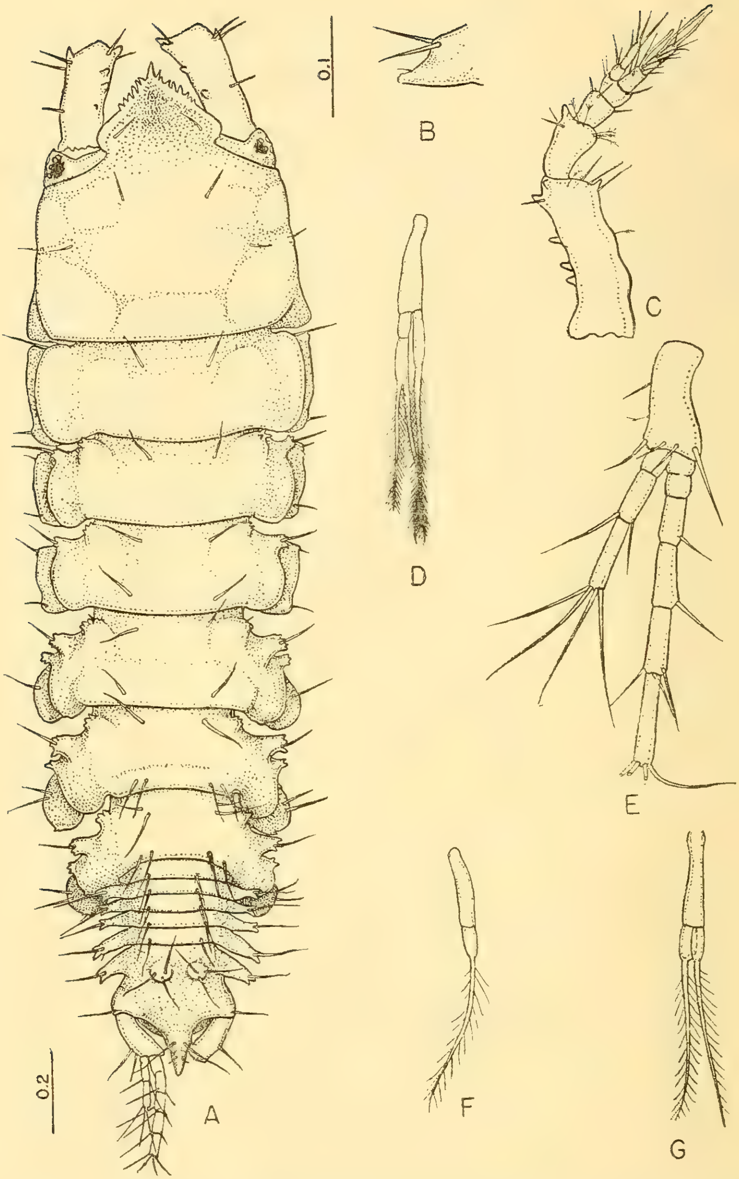

Fig. 25. *Imitapseudes magdalenensis*, n. sp., paratype, A. toto, B. lateral view of telson, C. first antenna, D. first pleopod, E. uropod. *Imitapseudes veleronis*, n. sp., paratype, F. male first pleopod, G. female first pleopod. Figures with similar magnification, A, C; B, D, E, F, G.

Material examined (exclusive of types). PANAMA. *Piñas Bay,* January 29, 1935, 1 ovig. female, 2–4 fms., coral, AHF Sta. No. 444–35.

COLOMBIA. *Gorgona Island,* January 22, 1935, 1 ovig. female, shallow water, coral, AHF Sta. No. 411–35.

GALAPAGOS ISLANDS. *Charles Island,* January 17, 1934, 1 male, 3 fms., low tide, AHF Sta. No. 161–34.

Geographic range. Panama to Colombia, and the Galapagos Islands.

Remarks. Were it not for the fact that the pleopods of this species are so constant in their morphology, I would certainly have considered this species identical with *I. magdalenensis.* Until intergradations are found it is apparent that the two should be considered distinct species.

Genus CYCLOPOAPSEUDES new genus

Type species. Cyclopoapseudes indecorus new species.

Diagnosis. Pleon consisting of six somites including telson. Adult with five pairs of pleopods. Gnathopod and second peraeopod without an epipod. Second antenna with a scale. Mandibular palp triarticulate. Dactyl of second peraeopod with a simple, pointed apex. Somites of pleon all of similar width. Facet bearing separated eyelobes present.

Remarks. The lack of epipods and the peculiar *Cyclops*-like shape of the animal are the only apparent features separating this genus from *Apseudes.* These characteristics, of course, need not be of generic importance, but considering the facts that *Apseudopsis* is separated from *Apseudes* only because its ocular lobes are completely fused with the cephalon, and that *Parapseudes* is separated from *Apseudes* in having one less pair of pleopods, it would seem desirable to keep *Cyclopoapseudes* separate from *Apseudes* also.

To my knowledge no other species of apseudid has been described to date which can be placed with certainty in *Cyclopoapseudes.*

CYCLOPOAPSEUDES INDECORUS new species

Figures 26–27

Diagnosis. Eyes laterally located. Peduncle of first antenna with three articles; first exceeds two-times the length of second, third about one half as long as second. Inner branch of flagellum of first antenna

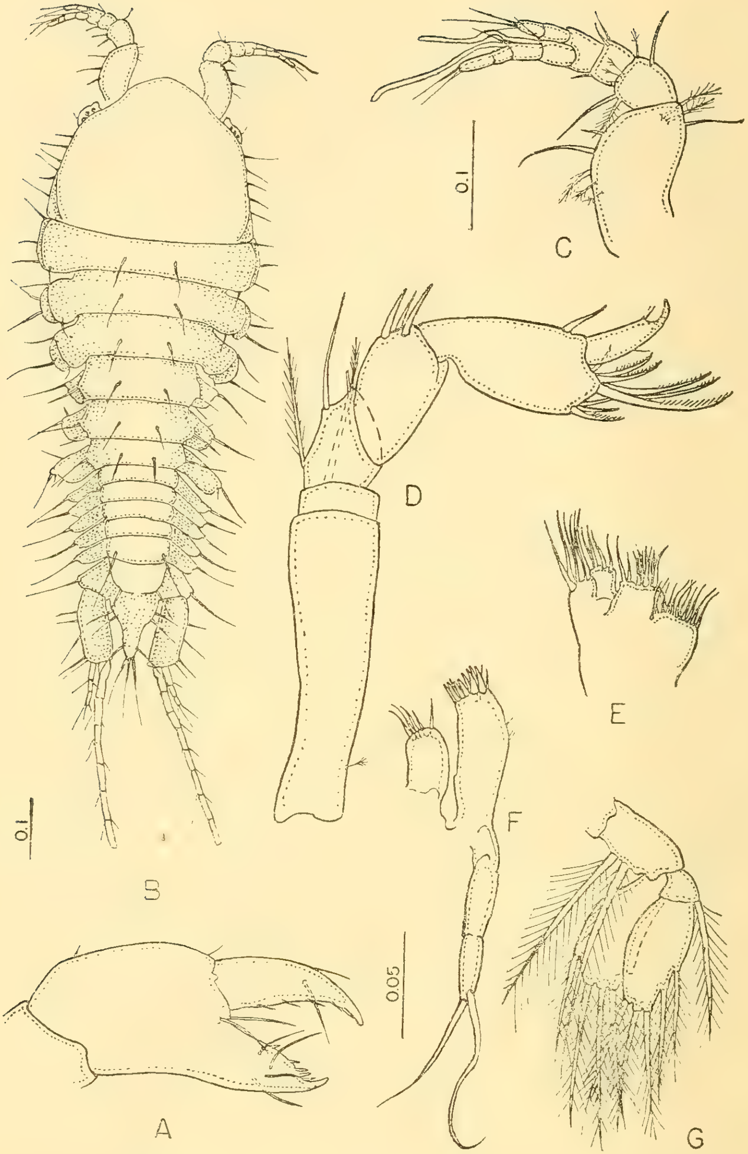

Fig. 26. *Cyclopoapseudes indecorus*, n. sp., holotype, A. gnathopod, B. toto, C. first antenna, D. fourth peraeopod, E. second maxilla, F. first maxilla. G. first pleopod. Figures with similar magnification, A, D, E, F, G; B; C.

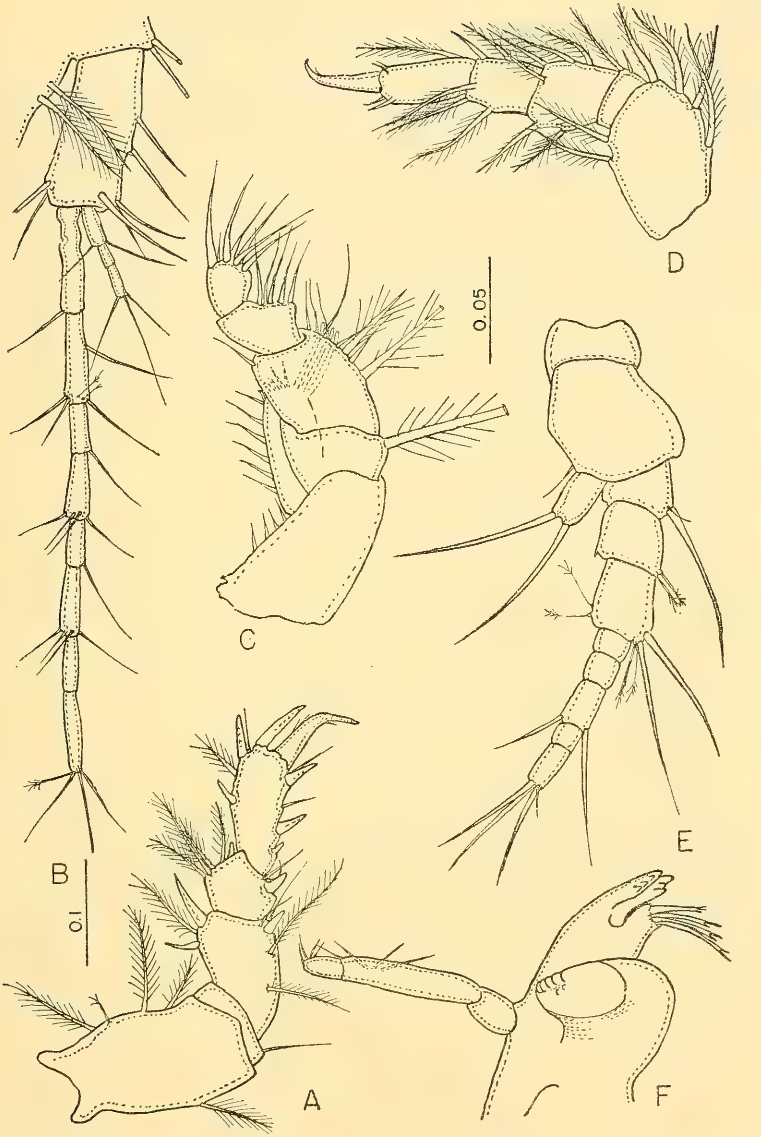

Fig. 27. *Cyclopoapseudes indecorus*, n. sp., holotype, A. second peraeopod, B. uropod, C. maxilliped, D. seventh peraeopod, E. second antenna, F. left mandible. Figures with similar magnification, A, B, D; C, E, F.

with two articles, outer with four. Second antenna with ten articles, scale small. Peraeonal and pleonal somites of similar length. Peduncle of uropods long, exceeding one-half the length of the telson; exopod with three articles, endopod with eight articles. Outer branch of pleopods with two articles. Third article of mandibular palp about one-fourth the length of the second and equal to the first in length. Incisor of right mandible with five teeth, that of left with four teeth, lacinia with at least three teeth, setal row with four setae.

Measurements. Holotype male, length 0.90 mm., width 0.35 mm.

Type locality. Ecuador, off La Plata Island, February 10, 1934, holotype, 7–10 fms., AHF Sta. No. 213–34, found with specimens of *Parapseudes pedispinis* (Boone).

Location of type. The type is deposited in the collections of the U. S. National Museum, Washington, D. C.

Material examined. Type only.

Geographic range. Known from type only.

Remarks. The abrupt narrowing of the fourth and fifth somites of the peraeon as shown in the figure may represent an aberrant condition. When the somites are spread out they are about equal in width to the other somites of the peraeon. The fourth pair of peraeopods seems excessively long and peculiar in structure in comparison with the fourth pair of peraeopods of other apseudids.

ADDENDUM

After the appearance of this paper in proof the writer received Dr. Sueo M. Shiino's excellent paper "On two new species of the family Apseudidae found at Seto." There Shiino described *Synapseudes setoensis* and *Metapseudes albidus,* both of which were collected from the intertidal zone on the rocky coast of Seto, Wakayama Prefecture Japan. *Synapseudes setoensis* is clearly related to *Synapseudes rudis* and *S. hancocki* in having a second antenna with six articles and a uropodal exopod with three articles. The mature male gnathopod of *S. setoensis,* like that of *S. hancocki* and unlike that of *S. rudis* lacks an apical claw on each finger. The dactyl of that gnathopod of *S. setoensis* has at least five marginal teeth on the cutting edge; whereas, that of *S. hancocki* has only three such teeth. The cheliped of less mature males of *S. hancocki* is markedly different from the cheliped of similarly developed *S. setoensis* in having teeth on the inferior margin of the dactyl; to judge from Shiino's figures "sub-adult" specimens of *S. setoensis* lack teeth on the inferior margin of the dactyl of the cheliped.

Shiino's excellent descriptions and figures are so complete that there is no doubt that his *Metapseudes albidus* belongs to my new genus *Imitapseudes*. *Imitapseudes albidus* (Shiino), as I shall here refer to that species, seems closely related to *I. magdalenensis* and *I. veleronis*. From these it differs (again to judge from Shiino's figures) in having the first two articles of the uropodal exopod subequal in length. In *I. magdalenensis* and *I. veleronis* the first article of the uropodal exopod is markedly shorter than the second. The endopod of the uropod of *I. albidus* has further about two more articles than are found in *I. magdalenensis* and *I. veleronis*. Like *I. veleronis* and unlike *I. magdalenensis*, the pleopods of *I. albidus* have uniarticulate rami. *I. albidus*, however, further differs from *I. veleronis* in that the females have biramous and not uniramous pleopoda. In summary, there seem several specific differences between the species described herein and those described by Shiino from Japan.

I can not concur with Shiino that *Metapseudes auklandae* and *I. albidus* belong to the same genus. The mere absence from *Metapseudes* of the antennular scale, of the pseudosegment on the pleotelson, and of the broad rostral plate seem to be pronounced differences of generic importance. *Apseudes*, *Apseudopsis*, and *Parapseudes*, three genera recognized as valid by most writers, seem obviously more nearly related to one another than *Metapseudes* is to *Imitapseudes*. As previously pointed out, *Apseudes* differs from *Apseudopsis* only in that the eyelobes are separated from the cephalon in the former and are fused with the cephalon in the latter. *Parapseudes* differs from *Apseudes* primarily in having one less pair of pleopods. As long as those genera continue to be recognized as distinct on such characteristics one must also consider *Imitapseudes* similarly valid.

LITERATURE CITED

Boone, P. L.

1923. New marine tanaid and isopod Crustacea from California. Proc. Biol. Soc. Washington. **36**: 147–156.

Bouvier, E. L.

1918. Sur une petite collection de crustacés de Cuba offerte au Muséum par M. de Boury. Bull. Mus. National Hist. Nat., **24**: 6–15.

Chilton, C.

1882. Additions to the isopodan fauna of New Zealand. Trans. Proc. N. Zealand Inst. 1882, **15** (1), Zoology, Art. X: 145–150, figs. 1–11.

Edwards, H. Milne

1828. Mémoire sur quelques crustacés nouveaux. Ann. Sci. Nat., **13**: 287–301, pls. XIII–XV.

Grube, A. E.

1864. Die Insel Lussin und ihre Meeresfauna. 116 pp., 1 pl., Breslau. (Not seen).

Hansen, H. J.

1895. Isopoden, Cumaceen und Stomatopoden der Plankton-Expedition. Plankton-Exped. Humboldt-Stiftung. 2, G, c: 1–105, 8 pls., Lipsius & Tischer, Kiel und Leipzig.

Haswell, W. A.

1882. Description of a new species of *Apseudes*. Proc. Linn. Soc. New South Wales. **6** (4): 748–749, pl. VI.

Lang, K.

1949. Contribution to the systematics and synonymics of the Tanaidacea. Ark. för Zool., **42A** (18): 1–14.

Leach, W. E.

1814. Crustaceology, *in* Brewster's Edinburgh Encyclopaedia, pp. 383–437, pl. 221. London.

Menzies, R. J.

1949. A new species of apseudid crustacean of the genus *Synapseudes* from northern California (Tanaidacea). Proc. U. S. Nat. Mus., **99** (3251): 509–515, figs. 41–42.

Miller, M. A.

1940. The isopod Crustacea of the Hawaiian Islands (Chelifera and Valvifera). Occ. Pap. Bernice P. Bishop Museum. **15** (26): 295–321, 9 text-figs.

Monod, Th.

1923. Sur un *Kalliapseudes* nouveau des Côtes Mauritaniennes. Bull. Soc. Zool. France, **48** (2–3): 132–137.

MONTAGU, G.

1808. Description of several marine animals found on the south coast of Devonshire. Trans. Linn. Soc. London. **9**: 81–114.

MOORE, H. F.

1901. Report on Puerto Rican Isopoda. U. S. Fish Comm. Bull. (1900), **2**: 161–176, pls. 7–11.

NIERSTRASZ, H. F.

1913. Die Isopoden der Siboga-Expedition. I. Isopoda Chelifera. Monographie XXXIIa. Siboga Expeditie, pp. 1–56, 3 pls., E. J. Brill, Leiden.

RICHARDSON, H. E.

1902. The marine and terrestrial isopods of the Bermudas, with descriptions of new genera and species. Trans. Conn. Acad. Sci., **11**: 277–310, pls. XXXVII–XL.

1905. A monograph on the isopods of North America. Bull. U. S. Nat. Mus., **54**, 727 pp., 740 text-figs.

1912a. Description of a new species of isopod belonging to the genus *Apseudes* from Ecuador. Proc. U. S. Nat. Mus., **42** (1918): 583–585, 1 text-fig.

1912b. Descriptions of two new isopods, an *Apseudes* and a *Munnopsis*, both from the Galapagos Islands. Proc. U. S. Nat. Mus., **43** (1926): 159–162, figs. 1–4.

RISSO, A.

1816. Histoire naturelle des crustacés des environs de Nice. 175 pp., 3 pls. Paris.

SARS, G. O.

1886. Nye bidrag til kundskaben om Middelhavets invertebratfauna. III. Middelhavets saxisopoder (Isopoda chelifera). Arch. f. Math. Naturvid., Kristiania. **5** (2): 263–368.

SHIINO, S. M.

1951. On two new species of the family Apseudidae found at Seto. Rept. Facult. Fisheries, Prefectural Univ. of Mie. **1** (1): 12-25, 6 text-figs.

STEBBING, T. R. R.

1910. Isopoda from the Indian Ocean and British East Africa. Percy Sladen Trust Expedition to the Indian Ocean in 1905. Trans. Linn. Soc. London. Ser. 2, Zool., **14** (1): 83–122.

VANHÖFFEN, E.
1914. Die Isopoden der deutschen Südpolar-expedition 1901–1903. Deutsche Südpolar-Expedition. **XV**, Zoologie VII, (4): 449–598, 132 text-figs. (G. Reimer, Berlin).

WHITELEGGE, T.
1901. Crustacea, part 2. Isopoda, part 1. *in* Sci. Res. Trawling Exped. H.M.C.S. "Thetis". Mem. Austral. Mus., **4** (3): 203–246, text-figs. 15–23.

WILLEMÖES-SUHM, R. VON
1879. On some Atlantic Crustacea from the Challenger Expedition. Trans. Linn. Soc. London, ser. 2, **5** (1), Zool.: 23–59.

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ON THE EARTHWORMS OF THE ARNOLD ARBORETUM, BOSTON

By G. E. Gates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
February, 1953

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No. 10. — *On the Earthworms of the Arnold Arboretum, Boston*

By G. E. Gates

TABLE OF CONTENTS

Page

Introduction 501

Family Lumbricidae 504

- Genus *Allolobophora* Eisen 504
  - *A. caliginosa* (Savigny) 505
  - *A. arnoldi* Gates 510
  - *A. molita* Gates 513
  - *A. chlorotica* (Savigny) 518
  - *A. limicola* Michaelsen 518
  - *A. longa* Ude 521
- Genus *Dendrobaena* Eisen 523
  - *D. octaedra* (Savigny) 523
  - *D. subrubicunda* (Eisen) 523
- Genus *Eisenia* Malm 523
  - *E. foetida* (Savigny) 523
  - *E. rosea* (Savigny) 524
- Genus *Eiseniella* Michaelsen 524
  - *E. tetraedra* (Savigny) 524
- Genus *Lumbricus* L. 525
  - *L. castaneus* (Savigny) 525
  - *L. rubellus* Hoffmeister 525
  - *L. terrestris* L. 527
- Genus *Octolasium* Örley 528
  - *O. cyaneum* (Savigny) 528
  - *O. lacteum* (Örley) 528

Family Glossoscolecidae 529

- Genus *Sparganophilus* Benham 529
  - *S. eiseni* Smith 529

Family Megascolecidae 529

- Genus *Pheretima* Kinberg 529
  - *P.* sp. 529

Discussion 530

Summary 533

References 534

INTRODUCTION

Various parts of the world have supplied live plants to the Arnold Arboretum of Boston, Mass. The soil around roots of plants imported in earlier days probably contained earthworms and/or their cocoons. The present contribution is based on collections primarily made to discover if any unusual exotic species that may have been so imported had been able to establish itself in the new environment.

The earthworms were obtained by digging, at various times from the middle of March to early in June, at the following six sites:

Peter's Hill. In black, saturated soil, below spring on side facing railroad.

Ponds. In leaf-covered mud under water at margins of ponds number one and two.

Natural woods. In a leaf dump. The leaves were of the previous autumn, Worms were obtained near periphery of a large pile and mostly in the first six to eight inches of material above the ground.

Manure heap. On high ground behind Bussey Institution.

Peat bog. At margin of spring-fed brook below administration building. Worms were collected from soil above as well as below level of water in brook. This area may be covered with water after heavy rains.

Railroad bog. In a low area by railroad tracks, sand, gravel, rock, stumps, logs, and other debris had been deposited. In several small depressions where grass did not grow, soil was covered with a litter of twigs, stems and some few leaves.

In addition, on the last day collecting was possible, worms were looked for under litter in groves throughout the arboretum, except in the bogs. In and under the thick litter beneath gymnosperms no earthworms were found. Under the litter beneath angiosperms worms were occasionally found. The day was hot and many of the specimens died before reaching the laboratory.

To provide material for comparison with the arboretum collections, worms were also secured from a small section of a garden on gravelly subsoil in Newton, Mass.

The soil in the arboretum is acid; a pH of 4.5 to 5.5 having been reported from various sites. In a sample taken from the collecting area in the peat bog in May the pH was 5.52.

Each specimen was checked for amputation, regeneration and homoeosis. Any externally recognizable abnormality in the clitellar region and anteriorly was recorded, but posteriorly, as a rule, only such metameric anomalies as were detected in segment counting.

In this contribution "clitellate" refers to worms with externally recognizable indications of clitellar development, including specimens in which first indications of epidermal modification (change in color and increase in thickness) are recognizable, as well as those in which an epidermal thickening is no longer recognizable but with site of clitellum marked by a special yellowish to brownish coloration. On many of the worms the clitellar thickening of the epidermis, even by end of May, apparently had not reached its maximum (see, in particular, note under *A. longa*). At that maximum the clitellum often cracks during preservation or on handling afterwards.

In a few worms, a half and/or a whole segment anterior or posterior to the clitellum showed some modification — epidermis translucent and perhaps slightly thickened. If a whole segment is involved the intervening intersegmental furrow is not obliterated. In nearly every case transition from region of slight thickening and of translucence to that of greater thickening and opacity is abrupt. This line of demarcation between opacity and translucence was taken as the clitellar boundary, the slightly modified translucent region not being included. Thus, in Table III, No. 5, xxvi has translucent epidermis; No. 24, xxvi and xxxv; No. 37, xxvii and xxxv.

In expressions such as "½28" or "½xxviii" the ½ is an approximation only.

Any worm with tubercula pubertates more or less clearly outlined but with no indication of past or present clitellar development is characterized as aclitellate. Whether any of such individuals are postsexual is unknown. Juvenile refers to any individual on which tubercula pubertates are unrecognizable or not certainly so, and, of course, with no indications of past or present clitellar development. Specimens without tubercula but with clearly recognizable though rudimentary genital tumescences are provisionally considered to be "late juveniles" (Table III).

Areas of epidermal modification around certain pairs of setae, but without externally recognizable, clearly marked boundaries, as in the case of the "genital markings" of many megascolecid and moniligastrid genera, are referred to as genital tumescences. Occasional absence of a tumescence on one side of a segment is not usually recorded except in case of certain variant individuals of the *caliginosa* complex.

Segments have long been designated, in oligochaetological literature, by Roman numerals, usually in lower case. In the tables of the present contribution, for the greater convenience of all concerned, Arabic numerals are substituted though conventional usage is followed in the text.

Location of the first dorsal pore, when definitely determined, is indicated in the usual manner. In front of the first obviously functional pore there may be one or more pore-like markings. Each of such markings is indicated by a "?". Thus, "????14/15" records the presence of pore-like markings, which may or may not be functional pores, on intersegmental furrows 10/11–13/14.

Amputee refers to any specimen that had lost a portion of the main axis, but without regeneration, regardless of whether amputation was produced by external or internal (autotomy) causes. Only posterior amputees were found in the Boston collections. In each case a new anal region had been formed that is more or less definitely demarcated from the last segment.

In one species, *L. terrestris*, after posterior amputation, the last few segments gradually acquire some of the characteristics of a normal tail (unpublished MS.). Possibly on completion of such a process it would be difficult, or perhaps even impossible, to distinguish the reorganized segments from a normal tail. If a similar reorganization takes place in other species, the incidence of amputees may be greater than has been indicated below, especially in species such as *L. rubellus* and *L. terrestris.*

"Head regenerate" means an anterior regenerate of cephalic nature without any connotation as to nature or segmental composition of a so-called "head".

Although copulation was several times observed, and in species in which that process has not yet been studied, no indications of cocoon deposition were noted. Only one cocoon was found during the collecting. However, no special attempt was made to sieve or otherwise manipulate the soil so as to secure cocoons.

Family LUMBRICIDAE

Genus ALLOLOBOPHORA Eisen 1874

The *caliginosa* complex

Peter's Hill, early May, 5 aclitellate and 14 clitellate specimens. (26 juveniles of various sizes probably belong here.)

Natural woods, May, 21 clitellate specimens. (28 juveniles of various sizes probably belong here.)

Peat bog, March–April, 2 aclitellate and 13 clitellate specimens. (15 juveniles probably belong here.) May, 2 aclitellate and 5 clitellate specimens.

Railroad bog, early May, 7 aclitellate and 27 clitellate specimens.

Newton, garden, April, 4 aclitellate specimens. (22 juveniles probably belong here.) Early May, 8 clitellate specimens.

From *A. caliginosa*, as it had long been understood, there have recently been split off *nocturna* Evans 1946 and *iowana* Evans 1948. Those three species were thought to be distinguished by differences in location of first dorsal pore, extent of male porophores, etc., and especially by number of segments, characteristics which had not previously been given such weight in lumbricid taxonomy. *A. nocturna* was further said to be distinguishable by physiological differences; feeding on surface of ground at night with tail anchored in burrow (as in *Lumbricus terrestris* L.), and an obligatory diapause (June–July) in sexual adults. Other distinctions from *caliginosa*, in case of *nocturna*, apparently are provided by the habit of depositing castings on the surface of the ground rather than below and by the production of new segments in post-embryonic growth after hatching (other English lumbricids, except *A. longa* Ude 1885, supposedly hatching with adult number of segments).

In a preliminary sorting of the arboretum collections, by elimination of all specimens obviously referable to other species, a residue, the *caliginosa* complex, was obtained. None of this material seemed to be referable either to *nocturna* or *iowana*. Yet there seemed to be considerable variation in characteristics of taxonomic importance. After some study it was found that most of the worms, and especially those with characteristic *caliginosa* tubercula pubertates, could be quickly separated into two batches according to the presence or absence of genital tumescences on xxxiii. The worms with tumescences on xxxiii can all be referred to *caliginosa* (*sensu stricto*) as now understood by

Evans, with only slight modifications of his diagnosis. For the worms with tumescences lacking on xxxiii a new species, *A. arnoldi* Gates 1952, was erected. To the two species *arnoldi* and *caliginosa* as now defined, it was possible to refer the remaining portion of the complex, mostly late juveniles, except for one specimen. That worm, with quadripartite tubercula on xxx–xxxiii, of band-shape, instead of somewhat reniform shape and double origin on xxxi–xxxiii, seemed to demand a new species, *A. molita* Gates 1952. In further collections listed below, most of the material was quickly referable to *caliginosa* or *arnoldi* but a few remaining specimens which should have gone into *molita* showed characteristics of *arnoldi* or *caliginosa.*

ALLOLOBOPHORA CALIGINOSA (Savigny) 1826

Peter's Hill, late May, 1 clitellate specimen.
Railroad bog, late May, 5 late juvenile, 6 aclitellate and 24 clitellate specimens.
Under litter, June 4, 1 clitellate specimen.
Newton, garden, late May, 6 aclitellate and 8 clitellate specimens. (Several younger juveniles probably belong here.)
(Peat bog, several specimens in earlier collections).

External characteristics. Length, 35–85 mm. Diameter, 1.5–4.5 mm. If an unusually small postsexual aclitellate worm (with tumescences on xxvii, xxx, xxxii–xxxiv) is left out, the measurements would be 60–85 x 3–4.5 mm. Segments, 125–168 (normal specimens). Pigmentation, if present sparse, a very light brown, more obvious in older, i.e., postsexual individuals than in those becoming sexual for first time. Apparently unpigmented worms have a rather greyish appearance, but when the gut is emptied such worms have a whitish appearance. Some of the appearance of color in other specimens may also be due to gut contents.

Genital tumescences are always present on ix–xi, (and with exceptions to be noted below) on xxx and xxxii–xxxiv. On 27 of the 67 specimens included in the table, tumescences are also present on xxvii, which is about 39 per cent. No specimen referred to this species has tumescences on xxvi as in *arnoldi.* Variation in external characteristics of taxonomic importance is shown in Table I.

Internal anatomy. The calciferous gland of xi is usually quite obviously larger than that of xii. The typhlosole has a flattened ventral surface on which there are three to five low, but definite longitudinal ridges.

Distribution. Worms of the *caliginosa* complex have been reported from Europe, Asia, Australia and New Zealand, South America and North America including many of the United States. The species as now restricted is known with certainty from Paris, France (the type locality), Rothamstead, England, Boston, Mass. and vicinity.

Life history. Some worms with no indications of clitellar development, either current or of a previous season, and on which tubercula are as yet unrecognizable, show quite clearly rudiments of genital tumescences. In absence of any other evidence of former sexual development these individuals are considered to be late juveniles. All worms with postsexual discoloration of the clitellar region have recognizable rudiments of the tubercula. In earliest recognized aclitellate individuals each tuberculum is clearly of double origin, represented by a slight tumescence of transversely elliptical outline confined to xxxi and xxxiii. In later stages each rudiment extends onto xxxii until the two come into contact on setal arc of xxxii. Even after considerable clitellar development a transverse depression, or groove or slight furrow may remain recognizable on that arc. Three of the clitellate specimens from the bog have spermatophores externally.

Amputation and *regeneration.* No anterior amputees or regenerates recognized. Of the worms included in the table nine or ten had undergone amputation posteriorly well prior to time of collection. Of those thus amputated, three or about 33 per cent had regenerated. Only around 4 per cent of the worms included in that table have tail regenerates (cf. with data for *arnoldi*). Segments in tail regenerates are as follows: at 72/73, 71; 101/102, 49; 104/105, 43.

Variant individuals. In these worms, unless otherwise indicated, genital tumescences are present on ix–xi. Certain other external characteristics are listed in Table II. The anterior margin of the clitellum is as in *caliginosa* except in No. 11 and No. 14 and then as in a number of specimens of *arnoldi*. Genital tumescences are on xxxiii, at least on one side, on each specimen except No. 12. Each specimen has at least one tuberculum of double origin and of same shape and location as in *caliginosa* (and also *arnoldi*). Variant tubercula need individual consideration.

No. 8. Each tuberculum is only slightly concave on the median margin but the concavity is deepest on setal arc of xxxii. There is no trace of depression, groove or furrow across the tuberculum. Except for the concavity in the median margin the shape would be band-like but wider than in *molita*.

No. 9. The left tuberculum is on xxxi–xxxiii but is band-shaped as in *molita*, median margin slightly incised at 31/32 and 32/33. No trace of those furrows recognizable across the tuberculum, and no incision, depression, groove or furrow on setal arc of xxxii.

No. 10. The right tuberculum is band-shaped, on xxx–xxxiii as in *molita*, but extends slightly onto xxix and xxxiv (median margin incised only at 30/31–32/33). A lateral portion is translucent but the median portion is opaque. (In a number of the specimens of both *caliginosa* and *arnoldi*, a median portion on each side of the concave portion of the tuberculum is quite opaque as contrasted with the translucence of the lateral part of the tuberculum.)

No. 11. The left tuberculum is band-shaped, on xxx–xxxiii, with incisions of median margin indicating four-part origin, as in *molita*.

No. 12. Both tubercula are as in *molita*, except that they are restricted to xxxi–xxxiii and median margins are incised only twice, at 31/32 and 32/33. There is no indication of furrow, groove, or depression on setal arc of xxxii. Genital tumescences on xxvii, as in so many specimens of *caliginosa*, suggest consideration here.

No. 13. The right tuberculum is lacking or unrecognizable. The specimen cannot be placed with reference to *arnoldi* and *caliginosa* by genital tumescences but the size, segment number, first dorsal pore, and anterior margin of the clitellum, all together seem to indicate *caliginosa*.

No. 14. Tubercula nearly normal but absence of tumescences on xxx and xxxiv raised a question. (Although the clitellum is only slightly developed, there are spermatophores externally and spermatozoa in the spermathecae.)

No. 15. The right tuberculum is just as in *molita*.

No. 16. The right tuberculum almost band-like as in *molita* but restricted to xxxi–xxxiii and with two halves clearly marked off by a groove along the setal arc of xxxii.

TABLE I

Variation in *A. caliginosa* (Savigny) 1826

Number of specimen	Number of segments	Extra tumescences on segment	Clitellum on segments	First dorsal pore on	Remarks	Locality
1	86	27	29–34	13/14	amputee	B
2	90	35	29–34	??13/14	amputee	N
3	96	*	#		amputee	
4	103	27	29–34	?	amputee	B
5	111	–	29–34	??13/14	amputee	B
6	112	*	#		amputee	
7	125	*	#	?12/13		
8	131	–	½28–½35	??13/14	no tumescence on 30	B
9	132	*	#	10/11		
10	133	*	#	?		
11	134	–	29–34	??13/14		B
12	135	*	#	?		
13	135	*	#	?		
14	135	–	29–34	???13/14		B
15	135	27	29–34	??12/13		B
16	136	–	a	11/12		N
17	136	27	a	?12/13		B
18	136	*	#	?12/13		
19	136	*	#	?		
20	136	27	29–34	??11/12		B
21	136	35	29–34	??13/14		B
22	137	27	29–34	?13/14		N
23	137	27	29–34	?13/14		N
24	137	–	½28–34	??13/14		B
25	138	27	29–34	??13/14	amputee?	B
26	138	27	29–½35	??13/14		B
27	139	*	#	?		
28	139	–	½29–½35	?		B
29	140	*	#	?		
30	140	–	29–34	??13/14		B
31	140	27	½28–34	?12/13		N
32	140	27	29–34	???13/14	no tumescence on 34	B
33	141	*	#	?		
34	142	–	a	??13/14		B
35	142	27	½28–34	??13/14		B
36	143	*	#	?		
37	143	*	#	?		
38	143	27	½28–34	??13/14	TR @ 72/73	B
39	144	*	#	?		
40	144	*	#	?11/12		
41	144	–	a	?12/13		N
42	144	27	½28–34	??13/14		RB
43	146	*	#	?		
44	146	27	29–34	??12/13		B
45	146	27	a	?13/14	probably postsexual	N
46	146	27	29–34	?11/12		B

TABLE I (*Continued*)

Number of specimen	Number of segments	Extra tumescences on segment	Clitellum on segments	First dorsal pore on	Remarks	Locality
47	147	*	#	?		
48	147	*	#	?12/13		
49	147	27	½28–½35	11/12		
50	147	–	½29–34	?12/13		N
51	147	27	29–34	??13/14	TR @ 104/105?	B
52	147	–	29–34	?12/13		B
53	148	27	29–34	?12/13		N
54	148	27	29–34	?13/14		N
55	149	27	29–½35	?12/13		P
56	149	*	#	?12/13		
57	149	–	a	??13/14		N
58	150	27	29–½35	?12/13	TR @ 101/102?	B
59	152	–	a	13/14		N
60	152	*	#	?		
61	154	*	#	?		
62	154	–	28–½35	?13/14	tumescences on 31 & 35	
63	154	–	29–34	??13/14		B
64	158	27	a	?12/13		B
65	162	–	29–34	?14/15		N
66	165	27	a	?13/14		N
67	168	27	29–34	?14/15	clitellum regressing	N
	120–150		½28, 29–34	11/12 or 12/13	Evans	England

* In 16 clitellate specimens so marked above there were nine with tumescences on xxvii.
# In 16 of the specimens so marked above a clitellum was present; from ½xxviii (3), xxviii (12), ½xxix (1) to xxxiv (11), ½xxxv (5).
B Bog.
N Newton garden.
RB Railroad bog.
P Peter's Hill.
TR @ 72/73. Tail regenerate at 72/73.
a Aclitellate.

TABLE II

External characteristics of variant individuals

	Number of specimen	Number of segments	Tumescences on segments	Clitellum on segments	First dorsal pore on	Remarks	Locality
A. arnoldi	1	179	R31, 32 L30, 32, 34	27–35	??12/13		P
	2	161	30, 32, 34	29–35	?12/13	TR @ 116/117	N
	3	138	0	R½27–½34 L28–34	???13/14	TR @ 117/118 and amputee	N
	4	159	L30, 32	27–34	9/10	75 x 4.5 mm.	RB
	5	160	R30, 32, 34	28–34	??11/12	80 x 5 mm.	RB
	6	172	R30, 32, 34	28–34	???1/12	90 x 5 mm.	RB
	7	168	L30, 32, 34	a	?11/12	TR @ 146/147 90 x 4.5 mm.	RB

TABLE II (*Continued*)

A. caliginosa	8	151	30–34	29–34	12/13	70 x 3 mm.	N
	9	151	L26, 27, 33 R30, 32, 33	a	?11/12		N
	10	124	L30, 32–34 R30, 33–34	29–$\frac{1}{2}$35	?11/12	60 x 3.5 mm. amputee	N
	11	154	L31 R30, 32–34	28–34	??13/14	85 x 4.5 mm.	RB
	12	140	27	29–34	??13/14	60 x 3 mm.	N
	13	144	L30, 32	29–34	?13/14	72 x 4 mm.	RB
	14	136	32–33	28–34	???13/14		RB
	15	141	L27, 32–33 R32–34	a	???13/14		RB
	16	136	L30, 32–34 R32–33	a	??13/14	65 x 3.5 mm.	RB

R Right side only.
L Left side only.
0 None.
??12/13 First definitely functional pore on 12/13 but more or less porelike markings on 10/11–11/12.
TR @ 116/117 Tail regenerate at intersegmental furrow 116/117.
75 x 4.5 mm. Length 75 mm., diameter 4.5 mm.
a Aclitellate.
P Peter's Hill.
N Newton garden.
RB Railroad bog.

ALLOLOBOPHORA ARNOLDI Gates 1952

Railroad bog, late May, 22 juvenile, 3 aclitellate and 24 clitellate specimens.
Peter's Hill, late May, 1 juvenile and 11 clitellate specimens.
Under litter, June 4, 1 clitellate specimen.
Newton, garden, late May, 20 juvenile, 8 aclitellate and 32 clitellate specimens.

External characteristics. Length, 55–100 mm. Diameter, 4–6 mm. Segments, 146–194 (normal specimens). Variation in characteristics of taxonomic importance is shown in Table III. Genital tumescences are always present on ix–xi, xxx, xxxii and xxxiv. On xxvi, tumescences are present in 21 (*ca.* 20 per cent) of the specimens included in the table, but on xxvii are present only on 2 (*ca.* 2 per cent) and on one of these there are tumescences also on xxvi.

Life history. Eight clitellate specimens from the railroad bog, six from the Newton garden, but only one from Peter's Hill had spermatophores externally. Some worms with only weak development of clitellum had spermatozoal iridescence (indicating copulation), in the spermathecae.

Amputation and *regeneration.* No anterior amputees or regenerates recognized. Of the worms included in the table, 43 (*ca.* 40 per cent) had undergone posterior amputation well prior to time of collection. Of those thus amputated more than 50 per cent had regenerated. Nearly 22 per cent of the worms included in the table have tail regenerates. Two of the specimens had again been amputated, through a regenerate. Amputation and regeneration certainly are not confined to the cultivated garden, nor, apparently, is their incidence in that garden significantly greater. These data, in comparison with those for *caliginosa,* may indicate that as a result of some different habit, within the same sites, *arnoldi* is more likely to lose part of its tail. The number of segments tends to decrease as level of regeneration passes posteriorly (see Table IV).

Abnormality and *homoeosis.* Abnormality, 3+. In one worm there are metameric abnormalities in the region of xiii–xxii, nevertheless genital tumescences are on xxx, xxxii and xxxiv on both sides. In another worm xii–xiii are involved in abnormality but again the clitellar tumescences are on the usual segments. A third worm has several metameric abnormalities behind the clitellum. Single metameric anomalies were observed on each of several other worms during counting of segments.

The single homoeotic is 72 x 4 mm., and with 155 segments. First dorsal pore on ?12/13. Clitellum on xxxi–xxxvi (+2?). Intestinal origin in xvii (+2). Gizzard in xix (+? +2). On the left side of the body conditions are as follows: spermathecal pores on 11/12–12/13. Female pore on xvi. Male pore on xvii. Genital tumescences on x, xi, xii (+1 only), xxxii, xxxiv, xxxvi. Calciferous sac in xii; gland in xiii only. Last heart in xiii. Testes and male funnels in xii–xiii; vesicles in xi–xiv. Ovary and female funnel in xv. On the right side conditions are as follows: spermathecal pores on 10/11–11/12. Female pore on xv. Male pore on xvi. Tumescences lacking. Calciferous sac in xi; glands in xii–xiii. Last heart in xii. Testes and male funnels in xi–xii; vesicles in xi–xiii only. Ovary and female funnel in xiv.

In this worm the homoeosis is quite unusual, being posterior (much more rare than anterior), asymmetrical, quite generally of one segment on the right and of two segments on the left (exceptions: lack of a seminal vesicle and one calciferous gland, the intestinal origin, gizzard and clitellum). There are no anomalies in the metamerism (of intersegmental furrows and septa). Symmetrical and total homoeosis, both anterior and posterior can be explained by hypomeric and hypermeric regeneration. At present it does not seem possible to explain the conditions in this specimen by regeneration. With the exception of the homoeosis (+2), conditions on the right side are characteristic of *arnoldi*.

Variant individuals. In these worms genital tumescences are present on ix–xi. Certain other external characteristics are listed in Table II. The anterior margin of the clitellum is as in *arnoldi* in each of the specimens except No. 2 (as in *caliginosa*). Clitellar genital tumescences are as in *arnoldi* on one side at least, in each case except No. 3 and No. 4. Each specimen has at least one tuberculum of double origin and of same shape as in *arnoldi* (and also *caliginosa*). Variant tubercula require individual consideration.

No. 1. The right tuberculum extends across xxx–xxxiii, with median margin slightly concave but no other indication of double origin and no incisions at sites of intersegmental furrows.

No. 2. Each tuberculum is continued well onto xxxiv but double origin is indicated by a slight groove along setal arc of xxxii.

No. 3. The right tuberculum is of characteristic *caliginosa-arnoldi* shape and of double origin, but is located on xxx–xxxii with the transverse groove on setal arc of xxxi, i.e., one segment anterior to normal location. The left tuberculum is band-like, reaching slightly onto xxx and xxxiv, apparently of triple origin as median margin is slightly incised at 31/32 and 32/33. No metameric abnormalities are recognizable in ventrum of clitellar region where intersegmental furrows and setae are visible.

No. 4. The right tuberculum is band-like, on xxx–xxxiii, of four-part origin as indicated by definite incisions of median margin at 30/31, 31/32 and 32/33, just as in *A. molita*.

No. 5. The left tuberculum is on xxxi–xxxiii and of double origin as indicated by a slight groove on setal arc of xxxii, as in *arnoldi*, but is band-like and in shape like the tubercula of *molita*. (The clitellar glandularity is only slightly developed and there is no spermatozoal iridescence on the male funnels. Nevertheless spermatophores are present externally and the spermathecae, in x and xi, have a spermatozoal iridescence. Copulation must have taken place even though clitellum is in a very early stage of development.)

No. 6. The left tuberculum is band-like but extends only from setal arc of xxxi to 33/34. Double origin is indicated by a slight depression on setal arc of xxxii. The shape is that of *molita*, the double origin as in *arnoldi-caliginosa*, the segmental extent foreshortened even for the two last species.

No. 7. The right tuberculum is band-like, on xxx–xxxiii, apparently of four-part origin as indicated by incisions of median margin at 30/31, 31/32, 32/33, which appear to be continued, rather faintly, across the tuberculum. This tuberculum is the same as in *molita*. (Although no trace of clitellar development is recognizable the male funnels are iridescent — indicating presence of mature spermatozoa. Iridescence in the spermathecae showed that copulation had taken place!)

ALLOLOBOPHORA MOLITA Gates 1952

Natural woods, May, 1 clitellate specimen (type).
Railroad bog, late May, 1 clitellate specimen.

The second specimen is characterized as follows: length, 65 mm. Diameter, 3.5 mm. Segments, 136. First dorsal pore, ??12/13. Clitellum, on $\frac{1}{2}$xxviii–xxxiv. Tubercula pubertates quadripartite, on xxx–xxxiii, median margins incised at 30/31–32/33. Genital tumescences on xxxii, xxxiii, xxxiv. Although the clitellum is only slightly indicated male funnels are iridescent, while iridescence in the spermathecae shows that copulation had taken place.

Remarks. One specimen, which cannot be placed in either *caliginosa* or *arnoldi*, by its genital tumescences, is tentatively assigned to *molita*. This worm is characterized as follows: length, 75 mm. Diameter, 4.5 mm. Segments, 159. Pigment wholly lacking, pinkish alive, whitish preserved. First dorsal pore, on 9/10. Clitellum indicated only by a slight yellowish tumescence on xxvii–xxxiv. The right tuberculum is as in the other two specimens but a little wider. The left tuberculum is of double origin, extending somewhat onto xxx and xxxiv, the two portions not quite meeting at the setal arc of xxxii. Genital tumescences, except on ix–xi, are lacking on the right side, present on the left side on xxx and xxxii.

On another specimen (No. 12, Table II), both tubercula are of the *molita* band shape but are tripartite with median margins incised at 31/32–32/33, and are restricted to xxxi–xxxiii as in *caliginosa* and *arnoldi*. As the only genital tumescences behind xi are on xxvii this specimen is tentatively assigned to *caliginosa.* (Iridescence in the spermathecae shows that this worm had copulated.)

Several worms with a quite characteristic *molita* tuberculum on one side, but with a more or less characteristically bipartite reniform tuberculum on the other side are tentatively referred to *caliginosa* (No. 10, No. 11, No. 15) or *arnoldi* (No. 4). Others with one tuberculum, or both, having some *molita* characteristics are similarly treated (see variant individuals under both species).

A specimen from southern France, identified as *caliginosa* by Gavrilov (1937, p. 146) had tubercula on xxx–xxxiii, but no further characterization as to shape and origin was given. Possibly tubercula of the *molita* type were present.

TABLE III

Variation in *A. arnoldi* Gates 1952

Number of specimen	Number of segments	Extra tumescences on segment	Clitellum on segments	First dorsal pore on	Remarks	Locality
1	109	–	½27–34	?11/12	amputee	RB
2	115	28	27–34	??10/11	TR @ 111/112	P
3	124	–	27–34	?11/12	amputee	
4	126	–	27–½35	??13/14	amputee	
5	129	–	27–35	??12/13	amputee	P
6	130	25–26	27–34	??12/13	amputee	RB
7	131	–	27–½35	?11/12	amputee	P
8	133	–	j	?10/11	TR @ 130/131	RB
9	134	–	j	?12/13	amputee	P
10	134	–	½27–½35	?10/11	amputee	
11	134	26	27–½35	?	amputee	
12	135	–	?*	?10/11	amputee	
13	136	26	½27–34	??11/12	TR @ 104/105 and amputee	RB
14	139	26	28–½35	??12/13	amputee	N
15	142	–	27–½35	10/11	amputee	
16	143	26	27–34	?11/12	amputee	
17	143	–	½27–34	?11/12	Probable amputee	RB
18	144	–	27–½35	?	TR @ 108/109	
19	146	–	½27–34	?11/12	amputee	N
20	146	–	½27–½35	?11/12		N
21	146	–	½27–34	?11/12	TR @ 98/99	RB
22	148	–	a	?11/12		RB
23	148	–	27–34	??11/12	TR @ 53/54	N
24	148	–	½27–34	???13/14	amputee?	RB
25	148	–	½27–34	??11/12		RB
26	149	–	j	?11/12		
27	149	–	j	??12/13	TR @ 113/114	N
28	150	–	½27–34	???12/13		N

TABLE III (*Continued*)

Number of specimen	Number of segments	Extra tumescences on segment	Clitellum on segments	First dorsal pore on	Remarks	Locality
29	150	–	28–34	??11/12	amputee	N
30	152	–	?	?10/11		
31	152	–	?	?10/11		RB
32	152	–	28–34	?11/12		N
33	154	26	a	?		RB
34	154	–	27–½35	?11/12		
35	154	–	27–34	10/11		P
36	155	–	a	11/12		RB
37	155	–	28–34	??11/12		P
38	155	–	28–34	??11/12		RB
39	155	–	½27–½35	???13/14	TR @ 97/98	N
40	156	–	?	?10/11		
41	156	–	27–½35	??11/12		
42	156	–	28–34	??12/13		N
43	156	–	27–34	???13/14		N
44	156	–	½27–34	??13/14	amputee	RB
45	157	–	?	10/11		
46	157	–	?	?10/11		
47	157	26	j	?10/11	TR @ 106/107	N
48	157	–	28–34	??12/13		N
49	158	–	½27–½35	?11/12		N
50	159	–	(27–34?)	10/11		
51	159	–	28–½35	???13/14	TR @ 90/91	N
52	159	26–27	28–34	?11/12	TR @ 130/131	RB
53	159	–	½27–34	?11/12	amputee	N
54	160	–	?	?11/12		
55	160	–	?	?12/13		
56	160	–	?	?10/11		
57	160	26	½27–½35	?10/11		
58	160	–	?	?10/11		
59	160	–	½27–½35	??11/12		RB
60	160	–	½27–34	10/11	TR @ 103/104	RB
61	160	–	(28–34?)	??11/12	TR @ 120/121	N
62	161	–	?	?		
63	161	26	½27–34	??11/12		RB
64	161	–	28–34	?11/12	amputee	RB
65	162	–	j	?11/12		RB
66	162	–	j	?11/12		RB
67	162	–	½27–34	?10/11		RB
68	162	–	½27–34	?11/12		RB
69	163	–	½27–½35	??11/12		N
70	163	26	½27–½35	11/12		
71	163	–	28–½35	?11/12		P
72	163	–	28–34	???13/14	TR @ 132/133	RB
73	164	–	a	?11/12	SP	RB
74	164	–	28–34	??13/14		P
75	165	26	j	10/11		
76	165	–	27–34	?11/12		N

TABLE III (*Continued*)

77	166	–	a	10/11		N
78	166	–	27–½35	11/12		P
79	166	–	½27–34	??11/12		N
80	166	–	27–34	??11/12		N
81	167	–	27–34	??11/12		RB
82	167	26	27–34	11/12	TR @ 113/114	N
83	168	–	27–½35	11/12		
84	168	–	j	10/11		RB
85	168	–	a	?11/12		N
86	169	26	28–34	???13/14		N
87	169	26	27–34	??11/12	TR @ 132/133	N
88	170	–	28–½35	?10/11		
89	170	–	½27–34	12/13		RB
90	170	26	½27–34	12/13		N
91	171	26	½27–34	??12/13		N
92	172	26	28–33	??12/13		N
93	173	–	27–½35	?10/11		
94	173	–	a	??11/12	TR @ 148/149	N
95	174	26	27–½35	?11/12		
96	174	26	27–34	?11/12		RB
97	174	–	28–34	??12/13	TR @ 89/90	RB
98	175	–	(28–34?)	?11/12	TR @ 138/139	N
99	175	27	½27–34	?	TR @ 126/127	N
100	176	–	28–34	??11/12	TR @ 130/131	N
101	178	–	½27–½35	?13/14	TR @ 83/84	P
102	178	26	½27–½35	?11/12		P
103	179	–	27–½35	?11/12		
104	184	–	a	??13/14	TR @ 120/121	N
105	187	–	½27–34	???13/14		N
106	194	–	?	12/13		

RB Railroad bog.
P Peter's Hill.
N Newton garden.
TR @ 111/112 Tail regenerate at 111/112.
j Juvenile, late, tubercula pubertates not certainly recognizable.
a Aclitellate.
?* Clitellar development had begun but anterior and posterior boundaries uncertain. Indicated in subsequent portion of the table merely by a "?".
(27–34?) Clitellar boundaries still doubtful but apparently at 26/27 and 34/35.
SP In this specimen, although no trace of clitellar development is recognizable, spermatophores are present externally and spermathecae are iridescent. Quite obviously copulation had taken place.

TABLE IV

Number of segments in tail regenerates of *A. arnoldi*

Level of regeneration	Number of segments in tail regenerates	Locality
53/54	95	N
67/68	57	B
67/68	95	B
69/70	44+	RB

Table IV (*Continued*)

76/77	78+	P	
83/84	95	P	
86/87	24	B	
87/88	83	RB	
89/90	85	RB	
90/91	69	N	
97/98	58	N	
98/99	48	RB	
99/100	88	RB	
103/104	45	B	
103/104	57	RB	
104/105	22+	RB	
106/107	51	N	
108/109	32	P	
111/112	4	P	
113/114	36	N	
113/114	54	N	
115/116	51	W	
118/119	48+	RB	
120/121	40	N	
120/121	64	N	
123/124	43	B	
125/126	45	P	
126/127	49	N	
130/131	3	N	
130/131	29	RB	
130/131	46		
132/133	31	RB	
132/133	37	N	
138/139	37	N	
142/143	36		(115/116)
148/149	25	N	
153/154	26	RB	

N Newton garden.
B Peat bog.
RB Railroad bog.
P Peter's Hill.
W Natural woods.
+ Amputee. Part of tail regenerate had been amputated prior to collection. Healed, but no regeneration.
(115/116) A previous regeneration at 115/116.

ALLOLOBOPHORA CHLOROTICA (Savigny) 1826

Railroad bog, under litter, late May, 2 juvenile and 2 clitellate specimens.

Segments, 102, 113 (j), 119, 128 (j). Bright green. Clitellum, on xxix–½xxxvii (1), xxx–½xxxvii (1). Genital tumescences, including *ab*, on xxxvii (1).

Spermatophores were present on one of the clitellate worms.

A. chlorotica has been reported from New England once before, from Connecticut, but without further indication of locality.

ALLOLOBOPHORA LIMICOLA Michaelsen 1890

Peat bog, March–April, 5 aclitellate and 65 clitellate specimens. May, 5 aclitellate and 39 clitellate specimens.

Railroad bog, early May, 1 juvenile, 5 aclitellate and 1 clitellate specimens. Late May, 1 juvenile and 9 clitellate specimens.

External characteristics. Length, to 100 mm. Diameter, to 4 mm. Segments (of 16 normal specimens): 98 (1), 107 (1), 113 (1), 118 (2), 120 (2), 122 (1), 123 (3), 124 (2), 125 (1), 126 (1), 127 (1). Pigmentation, lacking. Prostomium, epilobous, *ca.* ½, tongue open. Posterior end of body not tapering nor flattened, truncate, anal segment usually not visible in side view, as if retracted, and next segment often only partially visible in side view, as if also involved in the anal retraction. Setae may or may not be recognizable on the penultimate segment. Occasionally a peripheral portion of the anal segment is partially delimited by an incomplete furrow as if to mark off a rudiment of a new segment. First dorsal pore, in 4/5. Setae paired; the lateral a little more closely than the ventral; $ab > cd$, $aa > bc$, dd about = ½C. Nephropores, when recognizable, on or near *cd* lines.

Spermathecal pores, on 9/10–10/11, on *c* lines. Female pores, on xiv, on setal arc, slightly lateral to *b*. Male pores, in a transversely slit-like depression of a marked tumescence which extends nearly to *b* and *c* and to setal arcs of xiv and xvi, obliterating 14/15 and 15/16.

Clitellum, on ½xxix–xxxv (10), xxx–xxxv (49), xxx–½xxxvi (2), xxx–xxxvi (3), in earliest stages recognizable only on xxxi–xxxiv or xxxv. Ventral margins, as indicated by disappearance of clitellar opacity, about at level of lateral margins of tubercula, in mid *bc*. Tubercula pubertates, on xxxiii–xxxiv (except on variant specimens considered below), with bilobed median margin, incision at site of

33/34. In earliest stages each tuberculum is represented by two swollen areas, of shortly elliptical outline, not quite in contact at 33/34.

Genital tumescences, include *ab*: on ix (85), xi (84), xii (97), xxix (28), xxx (71), xxxi (70), xxxii (104), xxxv (89), xxxvi (31), xxxvii (13). In 14 specimens the region of *ab* of one side of x appeared to be slightly swollen, and in another worm there seemed to be a slight tumescence on each side of x.

Internal anatomy. Calciferous sacs, paired, large, in x (10). Calciferous glands, in xi–xii (10). Intestinal origin, in xv (10). Typhlosole, begins gradually in region of xx, at maximum development nearly filling intestinal lumen, gradually decreasing in size posteriorly. An anterior portion looks like a pile of coins with a string on the ventral face but posteriorly the lateral lamellae gradually disappear. The typhlosole ends abruptly in region of ciii–cix: ciii, worm with 118 segments; civ, with 124 segments; cix, with 125 segments. Last hearts in xi (10). Often there appears to be a pair of hearts in xii, as large as or larger than those of xi, but the vessels pass from the dorsal trunk anteroventrally, through 11/12 and then anteriorly median to the hearts of xi. Subneural trunk present.

Seminal vesicles, in ix–xii (10), those of ix–x smaller and often with brownish masses therein. Spermathecae project forward freely into ix and x and, when filled with sperm, may touch 8/9 and 9/10 or even be bent upwards.

Distribution. Previously reported from: Hamburg, (and Holstein?) Germany; Zürich, Switzerland; and three towns in Belgium. Original home still unknown.

Life history. Through early May at least, the clitellum of these worms seemed not to be fully developed, the epidermal thickening often less pronounced than might be expected, and rudiments of intersegmental furrows still faintly visible. Nevertheless 11 of the early May specimens had spermatophores externally, and other worms had spermatozoa in the spermathecae, showing that copulation had taken place.

Amputation and *regeneration.* Posterior amputees, 6 (+1?). Posterior regenerates, 1— of 11 segments, at 104/105. Probably a few segments only had been lost in each case.

Abnormality and *homoeosis.* Metameric abnormality: involving xi–xvi and probably result of some parietal damage; v–vi split on right side and in addition a spiral abnormality posteriorly; in xii–xviii;

spiral abnormality involving xxxiii–xxxv. Several other specimens had metameric abnormality in a postclitellar portion of the body.

Parasites. Several of the May specimens had parasitic masses in coelomic cavities of various segments in a postclitellar portion of the body. As yet there had been no extensive accumulations of such masses in the last few segments. Autotomy following accumulation of such masses seems to be an adequate explanation for the cases of posterior amputation observed.

Remarks. In the arboretum sites at which *A. limicola* was obtained, no castings were found. Presumably all intestinal ejecta are deposited underground.

Variant individuals

Peat bog, March–April–May, 4 aclitellate and 15 clitellate specimens.

Segments, (of four normal worms): 123 (2), 124 (1), 129 (1). Clitellum, on ½xxix–xxxv (2), ½xxix–½xxxvi (3), xxx–½xxxvi (4), xxx–xxxvi (5), xxxi–xxxv (1, but clitellar glandularity only very slightly developed). Tubercula pubertates, on clitellate worms, extending also across xxxv, as well as xxxiii–xxxiv; on left side only (4), on right side only (2), on both sides (9). On each of the six asymmetrical specimens that portion of the tuberculum on xxxv is slightly smaller than the other two parts, not reaching as far mesially as on xxxiii and xxxiv. A similar condition prevails on xxxv of two of the symmetrical clitellate specimens. On other clitellate individuals the tubercula have a trilobed median margin, incised at 33/34 and 34/35. On four aclitellate worms, with intersegmental furrows as yet uninterrupted, tubercula are each clearly composed of three equisized circular portions. Genital tumescences, of 15 normal specimens: on ix (15), xi (13), xii (15), xxix (3), xxx (12), xxxi (11), xxxii (14), xxxv (9 + 1?), xxxvi (8 + 1?), xxxvii (5). One worm appeared to have a tumescence on one side of x.

The typhlosole ends in civ, in worm with 123 segments; cv, in worm of 124 segments; cix, in worm of 123 segments; cxii, in worm of 129 segments.

Spermatophores were present on one of the May worms.

Posterior amputees, 2. Posterior regenerates, 1 — of 12 segments at 101/102.

Abnormality. Two specimens have metameric abnormalities in a postclitellar region of the body.

Remarks. The asymmetrical specimens with a tuberculum of one side limited to xxxiii–xxxiv as in the worms previously characterized, provide a transitional condition between the symmetrical worms with tripartite tubercula and those with bipartite tubercula. In these circumstances naming of worms with one or both tubercula tripartite seems unnecessary.

ALLOLOBOPHORA LONGA Ude 1885

Railroad bog, early May, 7 clitellate specimens. Late May, 1 juvenile, 1 aclitellate and 6 clitellate specimens.

Peter's Hill, late May, 22 juvenile, 4 aclitellate and 3 clitellate specimens. (16 other juveniles probably belong here.)

Newton, garden, April, 7 aclitellate and 1 clitellate specimens. Early May, 21 clitellate specimens. Late May, 1 clitellate specimen.

Segments, 183, 186, 193, 203. The posteriormost segments have a tendency to flatten dorsoventrally somewhat as in *L. terrestris* L., though not so marked as in that species. Pigmentation, brown. Two specimens from Peter's Hill had a deep blue appearance anteriorly and several others had a less marked bluish appearance of that part of the body. Clitellum, on $\frac{1}{2}$xxvii–xxxv (2), xxviii–xxxv (8), xxix–xxxv (1). Tubercula pubertates, on xxxii-xxxiv, except on one worm on which the right tuberculum extended across all of xxxv, the left reaching slightly onto xxxv. Genital tumescences, include *ab*, (of 48 worms): on viii (2), ix (48), x (48), xi (48), xxviii (4), xxix (2), xxx (1), xxxi (45), xxxiii (47), xxxiv (47). Male tumescences obliterate 14/15 and 15/16.

Distribution. A. longa has been reported once each from Maine and Connecticut but without further specification as to locality, and from Greencastle, Indiana.

Life history. On a number of worms, with no indications whatever of development of clitellum or tubercula pubertates, rudiments of genital tumescences are obvious, on ix–xi only, or also posteriorly. Most of the specimens characterized as clitellate actually have little or no tumescence of clitellar epidermis. Clitellar segments are however clearly indicated by a much darker brown or more yellowish coloration than that of other segments. On eight specimens only is the clitellum well developed.

Amputation and *regeneration*. One specimen had lost its first four segments, a ventral part of v, and a little of the anterior margin of vi ventrally. Missing parts of v–vi had been somewhat abnormally replaced and a new head of three segments regenerated. Another worm has a head regenerate at 3/4 but metamerism is abnormal (furrows quite irregular, setae and nephropores unrecognizable).

Tail regenerates are as follows: at 100/101, of 100 segments; 101/102, 98 segments; 117/118, 84 segments; 132/133, 70 segments; 133/134, 70 segments (juvenile from Peter's Hill); 136/137, 59 segments; 153/154, 29 segments; 154/155, 47 segments; 170/171, 14 segments.

Head regenerates have a uniform, light pinkish appearance, with delicate tissues, and presumably are of fairly recent age. Tail regenerates, on the contrary, all appear to be older though known recent tail regenerates of this species are not available for comparison. In France, in *A. longa,* head regeneration is supposed to be possible all year round with tail regeneration possible only during a summer diapause. Presumably then the two heads had been regenerated during the winter and the tails during the previous summer.

Amputations of the garden specimens can be attributed to cultivation. Some other agency presumably was involved in case of arboretum amputations for both sites from which they were obtained showed no indications of recent disturbance. The posterior amputations appear to have been too extensive for autotomy resulting from parasitic activity. Moles were not noticed. As earthworms of this species are supposed to cast on the surface of the ground, tails presumably could have been lost to birds while casting.

Remarks. Earthworms "throw up plenty of castings in the United States", according to Darwin (1881, p. 121). No authority was cited for that statement. We have to assume that the information on which it was based was obtained from correspondents who, quite probably, lived in a northeastern portion of the country. In that part of the States, only earthworms of the family Lumbricidae would be involved. Of the lumbricids of that region worms of only one species, *A. longa,* are known to deposit intestinal ejecta on the surface of the ground as "castings". As already noted above, that species has been reported but three times from the entire country. (Worms of one other lumbricid species, *A. nocturna,* are known to cast on the surface of the ground but that species has been recorded hitherto only from two localities in England.)

During the months of March-April-May, as well as in an early portion of June, little casting was observed in the Boston region. Such casts as were found were small in size, usually associated with rather small juveniles, and altogether seemed to be of insignificant volume especially in comparison with that to be seen in many parts of the oriental tropics after beginning of the rainy season.

In the Boston region, *A. longa* must have a fairly extended, externally imposed period of winter rest in addition to its internally imposed or obligatory summer diapause. Or, in colonizing a region with a different climate have ancient habits been modified?

Genus DENDROBAENA Eisen 1874

DENDROBAENA OCTAEDRA (Savigny) 1826

Under litter, June 4, 1 clitellate specimen.

Clitellum, on xxix–xxxiii. Tubercula pubertates on xxxi–xxxiii.

This specimen has no seminal vesicles.

DENDROBAENA SUBRUBICUNDA (Eisen) 1874

Manure heap, April, 1 clitellate specimen.
Railroad bog, May, 1 clitellate specimen.
Under litter, June 4, 3 clitellate specimens.

Clitellum, on $\frac{1}{2}$xxiv–$\frac{1}{2}$xxxii. Tubercula pubertates, on xxviii–xxx. Genital tumescences, on xvi (5), xxiv (1), xxvii (3), xxxi (3).

Genus EISENIA Malm 1877

EISENIA FOETIDA (Savigny) 1826

Manure heap, April, 29 clitellate specimens.
Under litter, June 4, 1 aclitellate and 15 clitellate specimens. (A number of other specimens died before reaching the laboratory and were not counted.)

All worms from the litter are slender and brevicaudate. The bands without the red pigment are inconspicuous in the manure worms, scarcely visible to unaided eye in worms from the litter. Genital tumescences, in front of xv, are too indistinct to be recognized with certainty. Behind xv, on worms from the litter, tumescences were recognized as follows: on xxi (3), xxii (8), xxiii (12), xxiv (4), xxv or xxvi to xxxii or xxxiii on each specimen.

Posterior amputees, 2. Regenerates, none.

The left tuberculum of one worm is on xxvii–xxix but the right is on xxviii–xxx (no abnormality of intersegmental furrows in clitellar region recognizable). One worm from the litter has a split metamere in the clitellar region. Every other worm from the litter has one or more metameric anomalies in the postclitellar region of the body.

Remarks. In the manure heap worms were present in great profusion, the 29 being from a single double handful of the manure, and apparently in good condition. In the litter, one specimen was found that had been dead for several hours at least (the only dead worm encountered in arboretum collecting) and other specimens from the same source seemed to be in poor condition.

EISENIA ROSEA (Savigny) 1826

Natural woods, May, 2 clitellate specimens.
Peat-bog, March–April, 2 clitellate specimens. May, 3 clitellate specimens.
Railroad bog, May, 1 clitellate specimen.
Newton, garden, late May, 1 clitellate specimen.

Segments, 115, 118 (peat bog). Clitellum, on $\frac{1}{2}$xxv–xxxii (8), xxv–$\frac{1}{2}$xxxii (1), xxv–xxxii (1). Tubercula pubertates, on xxix–xxx (1), on xxix–$\frac{1}{2}$xxxi (3, + 1 with tuberculum of one side extending clear across xxxi), xxix–xxxi (5). In latter case, each tuberculum is clearly marked off into three parts. Genital tumescences; including *ab*, of ix (2), xii (4), xxv (1), xxvi–xxxii (10), xxxiii (1); including *cd*, ix (1), x (1), xii (4), xiii (1). Tumescences of xxvi–xxxii are united or continuous with clitellar opacity except where tubercula intervene. A more or less definite furrow between tuberculum and tumescences may be continued all round the tuberculum.

Genus EISENIELLA Michaelsen 1900

EISENIELLA TETRAEDRA (Savigny) 1826

Ponds, April, 1 posterior fragment.
Peat bog, March–April, 1 clitellate specimen. May, 3 clitellate specimens.

Spermatophores were present externally on the May specimens. Clitellate worms are of the *forma* usually referred to as *typica*.

Genus LUMBRICUS L. 1758

LUMBRICUS CASTANEUS (Savigny) 1826

Natural woods, May, 3 clitellate specimens.
Peter's Hill, late May, under litter, 1 clitellate specimen.
Railroad bog, late May, under litter, 14 clitellate specimens.
Newton, garden, April, under leaf litter, 1 clitellate specimen.

Segments, 64 (amputee), 72 (amputee), 81 (Peter's Hill), 85, 88, 89, 90 (2), 91 (2), 92 (2), 93, 94 (2), 95. Clitellum, on xxviii–xxxiii (14), $\frac{1}{2}$xxviii–$\frac{1}{2}$xxxiii (2). Opacity extends about to the *a* line, occasionally *a* setae of xxix–xxxii included. Tubercula pubertates, on xxix–xxxii, with a narrowed extension of translucent portion onto anterior half of xxviii (16). Genital tumescences, include *ab*, on x (16), xii (1), xxiv (1). Tumescences are better developed or at least much more obvious than in *L. rubellus*.

Homoeotics, 2. In one the right female pore is on xiii and the right male pore is on xiv (bog). In the other (natural woods), all organs are one segment in front of the normal location. There are several metameric abnormalities in the postclitellar region. Presumably development had taken place in unfavorable conditions (metameric abnormalities resulting) and some time after hatching a posterior portion as well as an anterior portion had been amputated. The lost anterior part had then been replaced by a regenerate, hypomeric by one segment, which had become indistinguishable from the substrate. As the last segment (lxiv) had undergone little change, posterior amputation may have been more recent.

LUMBRICUS RUBELLUS Hoffmeister 1843

Natural woods, May, 3 aclitellate and 12 clitellate specimens. (18 juveniles may be of this species.)
Peat bog, March–April, 5 clitellate specimens. May, 2 juvenile, 2 aclitellate and 11 clitellate specimens. (3 juveniles probably belong here.)
Railroad bog, early May, 19 clitellate specimens. Late May, 4 clitellate specimens.
Ponds, April. (10 very small to small juveniles may be of this species.)
Under litter, June 4, 6 clitellate specimens. (Other specimens apparently of this species died before reaching the laboratory.)
Newton, garden, April, 10 clitellate specimens.

Segments, 58, 69, 78, 81, 84 (2), 93, 95, 98, 99, 101 (52 x 4 mm.), 106, 107, 108, 109 (2), 110, 111 (3, including one juvenile), 112 (3), 113 (2), 114, 115 (2), 116 (4), 117 (3), 119, 120 (2). In the peat bog series number of segments varied from 69 to 116, and in the railroad bog series from 93 to 120. A juvenile, 35 x 3 mm., and without indication of amputation, had 69 segments. The largest specimen, *ca.* 75 x 5.5 mm., had 116 segments. The anal segment in most specimens seems rather large, and is pigmented.

Clitellum, on xxvii–xxxi (2), xxvii–½xxxii (10), xxvii–xxxii (21), ½xxvii–½xxxii (5). Tubercula pubertates not distinct from but apparently united with the clitellum. In a number of specimens the ventral margin of clitellar opacity is slightly median to the *a* lines, with the *ab* setae of xxviii–xxxi included in the clitellum. In other worms the opacity does not quite reach the *b* lines. The tubercula of these specimens are recognizable only as translucent areas within the clitellar opacity. These translucent areas may be limited to xxviii–xxxi (3), or a narrowed extension may cross well into xxvii (35). On at least a dozen specimens vestiges of intersegmental furrows are recognizable across the translucent areas. Genital tumescences, include *ab*: on viii (3), ix (2), x (7), xi (17), xii (31), xiii (1), xi and xii (1), xxv (1), xxvi (35), xxvii (2), xxix (1), xxxii (1). Anterior to xv tumescences may be entirely lacking, or present only on one side of one segment, and often are only slightly developed and not easily recognizable.

Worms *in copula* were found in the leaf pile (natural woods) late in the morning of May fifth. Many of the clitellate specimens of the same lot had spermatophores externally.

Amputees, 2 only recognized as such. One posterior regeneration of a two-segment tail at 51/52 (Newton, garden).

Homoeotics, 2. In one, the left male pore is on xvi. Setae are lacking on left sides of xv–xvi but intersegmental furrows, septa and other organs are normal. On the other worm the right male pore is on xiv lateral to the female pore.

Remarks. A number of the specimens are obviously brevicaudate, with clitellum about at middle of the body. Even in those worms in which the clitellum seems well in front of the middle of the body, the number of segments is well below the species maximum of 150.

Lumbricus terrestris L.

Peat bog, March–April, 8 clitellate specimens. (8 juveniles may belong here.) May, 1 aclitellate and 1 clitellate specimens.
Natural woods, April, 10 clitellate specimens. May, 4 juvenile, 1 aclitellate and 10 clitellate specimens.
Peter's Hill, early May, 2 juvenile and 4 clitellate specimens. (5 small juveniles probably belong here.) Late May, 5 juvenile and 3 clitellate specimens.
Under litter, June 4, 1 clitellate specimen.
Newton, garden, late May, 5 clitellate specimens.

Length, 125–210 mm. Diameter, 7–12 mm. Segments, on juveniles of about adult size but without indication of sexual maturity: 149, 152, 155, 157. A somewhat smaller juvenile has 145 segments and one that is 120 mm. long has 108 segments, the last three of which apparently lack setae. Clitellate specimens from the bog (and Peter's Hill) are obviously brevicaudate; one, measuring 130 x 7.5 mm., has 98 segments. On none of the brevicaudate forms was evidence of posterior amputation or subsequent reorganization recognized.

Nephropores of a side, in Peter's Hill specimens, occasionally are in one location and in a nearly straight rank for several successive segments, as many as nine and eleven noted.

Clitellum, on xxxii–½xxxvii (1), xxxii–xxxvii (25), xxxii–½xxxviii (3), xxxii–xxxviii (1). Tubercula pubertates of aclitellate worms are markedly protuberant and obviously of quadripartite origin — intersegmental furrows still continued deeply across the tumescence. In clitellate specimens the tubercula are usually recognizable only as areas of sharply delimited translucence. In some cases a peripheral rim portion of opacity is more or less distinctly marked off. Tubercula reach across all or almost all of xxxiii–xxxvi (11), or reach slightly onto xxxvii (1), or across all of xxxvii (1, worm with clitellum reaching to 38/39). In other specimens, the tubercula, even including any specially opaque rim portion, fall quite definitely short of reaching 32/33 and 36/37. Genital tumescences, include *ab*: on xxv (9), xxvi (22), xxvii (2), xxviii (1), xxix (1), xxx (6), xxxi–xxxviii (32). Tumescences may also be present on some of segments vii–xii but if so are feebly developed and not certainly recognizable.

Amputees, none recognized. Regeneration: posterior, none; anterior, one. In this case (Newton, garden), i–iv and probably part of v on right side had been lost. The regenerate is a functional head, pinkish — without pigment, tissues still delicate. The prostomium is only slightly epilobous. Metamerism is quite abnormal, no normal intersegmental furrows at all, setae and nephropores lacking.

Abnormality and *homoeosis*, 3. In one worm the prostomium is practically prolobous. Pigmentation is normal and tissues are of usual firmness. If the unusual condition is due to regeneration, the regenerate is of an age as to be no longer recognizable as such. In another worm the left male pore is on xiv, lateral to the female pore. The left calciferous gland of xii is lacking (intersegmental furrows, septa and other organs normal). The third worm has eight spermathecal pores, about on the *c* and *d* lines of 9/10 and 10/11. Each of the eight spermathecae is markedly iridescent indicating presence of spermatozoa received in copulation. Each spermathecal duct is separated from that of its near neighbor by a sizable strand of longitudinal musculature.

Genus OCTOLASIUM Örley 1886

OCTOLASIUM CYANEUM (Savigny) 1826

Peter's Hill, May, 2 clitellate specimens.
Railroad bog, early May, 1 clitellate specimen.
Newton, garden, late May, 4 aclitellate and 2 clitellate specimens.

Segments, 151, 155. The last few segments, in living worms, were characterized by a brilliant yellowish appearance. During preservation most of the yellow masses responsible for that appearance were discharged from the coelomic cavities through the dorsal pores. Genital tumescences, include *ab*: on xviii (1), xx (1).

Distribution. O. cyaneum has been reported once before from this country, from Fairfield, Iowa.

OCTOLASIUM LACTEUM (Örley) 1881

Peat bog, March–April, 2 clitellate specimens. May, 1 clitellate specimen.
Peter's Hill, May, 3 clitellate specimens.
Newton, garden, late May, 3 clitellate specimens.

One of the worms from the Newton garden has a brownish coloration similar to that of *A. longa*. Genital tumescences, include *ab*: on xxi (4), xxii (6).

Worms *in copula* were found in the Newton garden late in the afternoon, in late May.

Each of the Peter's Hill worms has parasitic cysts in considerable numbers in the coelomic cavities of the postclitellar portion of the body. The single amputee, which had lost its tail at 96/97, may have autotomized the last segments to get rid of an accumulation of such parasitic masses.

Distribution. Reported once before in New England, from an unspecified locality in Connecticut.

Family GLOSSOSCOLECIDAE

Genus SPARGANOPHILUS Benham 1892

SPARGANOPHILUS EISENI Smith 1895

Ponds, April–May, over a hundred specimens.

Amputation and *regeneration.* In a series of 61 specimens: very recent amputees, posteriorly, 28; with small, unsegmented posterior regenerate about the size of one segment, 15; with a metamerically segmented tail regenerate, 9.

Although these worms appear to be unpigmented the substrate is sharply distinguished from the regenerate by an almost blackish appearance. One worm had been amputated posteriorly twice. The second regenerate is unsegmented but of quite different color from the first. One worm had lost a posterior portion of a regenerate very recently, possibly in collection. In fact all of the very recent amputees may have been broken in course of collection.

Parasites. A number of the worms had masses of parasitic bodies in the coelomic cavities of the postclitellar portion of the body.

Remarks. The longest of the worms with a normal posterior end has a very obvious and large growth zone in front of the anus.

Family MEGASCOLECIDAE

Genus PHERETIMA Kinberg 1866

PHERETIMA sp.

Under litter, June 4, 1 small juvenile.

Intestinal caeca, manicate.

Remarks. The only species of *Pheretima* hitherto found in Massachusetts (in greenhouses, near Northampton), *P. hawayana* (Rosa)

1891, has simple intestinal caeca. Two species with manicate caeca have been recorded from North America: *P. schmardae* (Horst) 1883, from the Bermudas and Barbados; and *P. agrestis* (Goto and Hatai) 1899, from Baltimore.

DISCUSSION

Eighteen species are represented among the thousand odd earthworms collected from only six sites within the confines of the Arnold Arboretum in the city of Boston. Of these species, *A. arnoldi, chlorotica, limicola, longa, molita, D. octaedra, O. cyaneum* and *lacteum* are recorded from Massachusetts for the first time, *A. limicola* for the first time outside of Europe, *A. arnoldi* and *molita* for the first time anywhere.

Most of the species that might have been anticipated were obtained, except the following: *Bimastos parvus* (Eisen) 1874, *B. tenuis* (Eisen) 1874, *Eisenia lönnbergi* (Michaelsen) 1894, each of which was already known from Massachusetts; *D. rubida* (Savigny) 1826, already known from Maine and New Hampshire, *Eisenia hortensis* (Michaelsen) 1890, California and Ohio, *Lumbricus festivus* Savigny 1826, several Canadian provinces, and *Dendrobaena mammalis* (Savigny) 1826, intercepted on plant materials imported into this country (Gates, MS). *A. limicola*, of course, as well as *arnoldi* and *molita*, were not anticipated. Nor was any species of *Pheretima* expected, as species of that genus have hitherto been known, in the colder parts of this country, mainly from greenhouses, as in the case of *P. hawayana* (Rosa) 1891 at Hadley, Mass. The important exception is *P. hupeiensis* (Michaelsen) 1895, from golf courses of western Connecticut to Washington, D. C.

Among the Lumbricidae of the arboretum are species such as *A. caliginosa* and *E. foetida* which seem to have been recognized almost everywhere that Europeans have settled. In several of such areas, that have been searched, about thirteen other lumbricids have been found. Occurrence of any of those fifteen species in the arboretum, accordingly, is of no particular significance; all may have been present in the Boston region before the arboretum was established late in the last century. Nor is importance attached to failure to find species such as *E. hortensis* or *B. parvus* in view of the limited number of sites studied and the small volume of material that was dug up or searched through.

The presence in the arboretum, and there alone, of *A. limicola* apparently is to be explained as a result of the introduction of exotic, live plants in soil. Other such introductions presumably have been responsible for presence of *Sp. eiseni* and the species of *Pheretima.*

The original sources of the 22 Massachusetts species must be looked for in three widely separated parts of the world. The most important, of course, is Europe which has provided all species of the genera *Allolobophora* (*arnoldi* and *molita* for the present considered to be of extra-American origin), *Dendrobaena, Eiseniella, Octolasium, Lumbricus,* and two species of *Eisenia.* Another source — southwest of New England and New York — has contributed *E. lönnbergi,* presumably one species of *Bimastos,*[1] and the glossoscolecid *Sparganophilus eiseni.* The last source, of the species of the megascolecid *Pheretima,* must be somewhere in that large area comprising Burma, Malaya, Thailand, Indo-China, China, Korea, and the islands of Japan, Malaysia, etc., but excluding Australia and New Zealand. (The two last, with India, Africa and South America, have apparently contributed nothing to the arboretum fauna.)

Some of the arboretum species appeared to be restricted as to habitat. Thus, *Sp. eiseni* was found only in bottom mud, *A. limicola* only in bogs, *L. castaneus* only under litter or in piles of decaying leaves, and *E. tetraedra* only in saturated soil. *E. foetida,* sold for ten years throughout the country as a garden, orchard or farm cultivator of the soil, was found only in manure or under thick leaf litter. Such few specimens of *D. octaedra, subrubicunda* and *A. chlorotica* as were obtained were also found only in manure and under or near litter.

Other species seemed to have no such restrictions, and were found in saturated bog soils, much drier garden soil, and, in certain cases, away from soil, in leaf piles. A number of such species were usually found in close neighborhood with each other as well as with those of more restricted habitat. In five of the sites the number of species varied from six to ten (see Table V). Almost certainly extension of collecting only a few feet in one direction or another would have yielded one to three more species in case of the railroad bog, Peter's Hill and the natural woods. As the table shows, nine species were obtained at three or more of those five sites, and two, *A. arnoldi* and *caliginosa,* at all of them. The one factor obviously common to all of those places was presence of a considerable amount of organic material (plant).

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[1] The other "species", *B. tenuis,* is at present, rather tentatively considered an athecal mutant of *D. rubida* and/or *subrubicunda.* Several specimens recently studied apparently can be so regarded (Gates, MS).

TABLE V

	Sites				
Species	Peat bog	Railroad bog	Peter's Hill	Natural woods leaf pile	Garden in Newton
A. arnoldi	+	+D	+	+	+D
caliginosa	+	+	+	+	+
chlorotica		+			
limicola	+D	+			
longa		+	+		+
D. subrubicunda		+			
E. rosea	+	+		+	+
tetraedra	+				
L. castaneus		+	+	+	+
rubellus	+	+		+	+
terrestris	+		+	+D	+
O. cyaneum		+	+	+	+
lacteum	+		+		+
Number of species	8	10	7	6	9

D, dominant

In each of the sites the earthworm population probably could be characterized as dense, somewhat less so perhaps in the Newton garden than in the other places.

A. limicola clearly was the dominant species in an apparently undisturbed portion of the peat bog next to the brook. The same earth from which all worms presumably had been removed in previous collecting was again dug over early in May. During the intervening period 50 (+) worms, of three species only, had moved into the disturbed soil. Of those, 44 were *limicola*, the rest belonging to the *caliginosa* complex. In the railroad bog, where there had been considerable filling, *A. limicola* was much less important, ranking fourth in the following series of descending order: *A. arnoldi, caliginosa, L. rubellus, A. limicola, longa. A. arnoldi* again appeared to be dominant in the Newton garden followed by *longa, caliginosa, rubellus* and *L. terrestris* in descending numerical importance. *L. terrestris* probably was dominant in the leaf pile of the natural woods, not only in number (only a few of the specimens that were seen having been brought to the laboratory and counted) but also in volume — all of the adults unusually large and many of them 2 to 3 mm. thicker than the maximum recorded by Cernosvitov and Evans (1947). Next in numerical order was the *caliginosa* complex and then *rubellus*. No specimens of *E. foetida* were found in that leaf pile or nearby. Yet, sometime later, some fifty or so feet away, under rather thick natural litter, *foetida* was found and in about the same number as *rubellus*.

In the leaf litter site of the natural woods, presence of one dead worm and of one or more metameric anomalies in every specimen examined, seemed to indicate some unfavorable factor in the environment, in spite of the numbers present. In other sites, worms appeared healthy and provided no indication of unusual incidence of homoeosis or abnormality in spite of low pH. However, the percentage of more or less obviously brevicaudate individuals in the leaf pile and bogs seemed unusually high.

In copulation, participating individuals always have been clitellate, in each species of earthworm that has been studied — *E. foetida, L. terrestris, Eutyphoeus waltoni* Michaelsen 1907, and *Pheretima communissima* (Goto and Hatai) 1899. A clitellum was also present on each individual of the copulating pairs of *L. rubellus* and *O. lacteum* mentioned on preceding pages.

It is therefore of interest that some arboretum specimens of *A. arnoldi* and *caliginosa* seemed to have copulated before development of the clitellum, or, in case of *A. limicola*, when the clitellum was only very slightly developed. Proof of copulation was provided by presence of "spermatophores" externally and of spermatozoa in the spermathecae. Iridescence on male funnels indicated, in at least one case, that the individual's own sperm had been mature.

After beginning of clitellar regression, in some species, presence of mature spermatozoa may still be indicated for some time by iridescence on male funnels and in spermathecae. No indications of clitellar regression were recognized in any of the arboretum specimens under consideration.

SUMMARY

Of 18 species collected in the arboretum, eight — *Allolobophora arnoldi, chlorotica, limicola, longa, molita, Dendrobaena octaedra, Octolasium cyaneum* and *lacteum* — are recorded from Massachusetts for the first time, *cyaneum* for the first time in New England, *limicola* for the first time outside of Europe, *arnoldi* and *molita* for the first time anywhere. A species of *Pheretima* was found outside of greenhouses

for the first time in Massachusetts. Presence of *A. limicola, Sparganophilus eiseni* and *Pheretima* sp. is considered to be the result of importation of live plants from three widely separated parts of the world. *A. limicola,* restricted to bogs, is dominant in an undisturbed peat bog, *arnoldi* in a bog with fill as well as in a Newton garden, *L. terrestris* both by number and volume in a leaf pile.

REFERENCES

CERNOSVITOV, L. and A. C. EVANS

1947. Lumbricidae. No. 6 in Synopses of the British fauna. London, Linnean Society.

DARWIN, C.

1881. The formation of vegetable mould through the action of earthworms. London, J. Murray.

EVANS, A. C.

1946. On a new species of earthworm of the genus *Allolobophora.* Ann. Mag. Nat. Hist. (11), **13**: 98–101.

1948. On some earthworms from Iowa, including a description of a new species. Ann. Mag. Nat. Hist. (11), **14**: 514–516.

GATES, G. E.

1952. New species of earthworms from the Arnold Arboretum, Boston. Breviora, **9**: 1–3.

GAVRILOV, K.

1937. Regenwürmer aus Südfrankreich. Zool. Anz., **118**: 145–154.

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A NEW FOSSIL TORTOISE FROM THE THOMAS FARM MIOCENE OF FLORIDA

By Ernest Williams

CAMBRIDGE, MASS., U. S. A.
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No. 11.—*A New Fossil Tortoise From the Thomas Farm Miocene of Florida*

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Several plastra, a nearly complete carapace and additional fragments of a tortoise from the Miocene of Thomas Farm, Gilchrist County, Florida, pertain to an undescribed form apparently ancestral to the giant tortoise of the Florida Pleistocene, *Testudo sellardsi.*

The new species may appropriately be named in honor of Dr. Theodore White whose work on other components of the Thomas Farm fauna is so well known:

TESTUDO TEDWHITEI, new species

Type. M.C.Z. No. 2020, a complete plastron.

Type locality. Thomas Farm, Gilchrist Co., Florida.

Horizon. Arikareean Miocene.

Diagnosis. With the characters of *Testudo sellardsi* Hay (as described by Loomis 1927) but much smaller, so far as known not exceeding 400 mm. in plastral length. Pectoral scute 1/6 to 1/7 the abdominal in length of median sulcus; gulars more triangular, anals smaller; nuchal scute well developed, reaching anterior margin; costo-vertebral sulci less deeply incised; free margins less reverted.

Referred material.

M.C.Z. No. 2021, "plastron 2".
M.C.Z. No. 2022, "plastron 3".
M.C.Z. No. 2023, "plastron 4".
M.C.Z. No. 2024, "plastron 5".
M.C.Z. No. 2025, a carapace lacking some of the left peripherals,

neurals 4 and 5, part of pleural 3 and all of pleural 5 of the left side.

M.C.Z. No. 2026, a miscellaneous lot containing three anterior carapace margins, a posterior lobe of a plastron, a small femur, a humerus, a scapula and acromion, and neurals, peripherals and other carapace fragments not further identified.

Character Analysis

1. A feature of considerable interest in the new species is the size of the pectoral scute, especially its medial anteroposterior dimension. In 1950 I used a difference in this dimension to assist in distinguishing Miocene *Hesperotestudo*[1] from Miocene *Gopherus* and Miocene *Chelonoidis*, ascribing to the first a pectoral scute with "median sulcus 1/15 to 1/30 of the abdominal median sulcus", to the second a pectoral scute with "a median sulcus usually about 1/5, never less than 1/10 of the abdominal median sulcus", and to the last a pectoral scute with the "median sulcus 1/5 the abdominal median sulcus". *Testudo tedwhitei* has the following measured values for pectoral and abdominal median sulci:

Specimen	pectoral	abdominal
type	20 mm.	116 mm.
plastron 2	20	118
" 3	17	114
" 4	18	129

This range of values gives ratios of approximately 1/6 to 1/7. According to the 1950 criteria this should rank *Testudo tedwhitei* either with *Gopherus* or with *Chelonoidis*. But in major characters the new Florida form is not a *Gopherus*, and the presence of a nuchal scute excludes it from *Chelonoidis*.

If we look now at Oligocene *Hesperotestudo* we find that *T. brontops* had the pectoral median sulcus between 1/4 and 1/5 that of the abdominal, while *T. amphithorax* had the same sulcus between 1/3 and 1/4 that of the abdominal.

Testudo tedwhitei is, therefore, intermediate in this character between the Oligocene species of *Testudo* and those Miocene species of *Testudo* which previously have been well enough known to be assigned definitely to the subgenus *Hesperotestudo*. Very fortunately we are not dealing here with a single specimen in which such an aberrant or apparently aberrant character might well be an individual variation. The pectoral-abdominal ratio is clearly shown in four specimens and readily inferred in a fifth. In this regard *T. tedwhitei* seems clearly to manifest as a species character a condition more primitive than that found in *T. osborniana* and its closer relatives. *T. sellardsi* as described by Loomis (1927) is nearer in this feature to *T. osborniana* than to *T. tedwhitei.*[1]

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[1] A subgenus of *Testudo* (type: *Testudo osborniana*, Miocene of Colorado) that includes all the North American members of the genus (Williams 1950). All living North American land tortoises belong to the genus *Gopherus*.

2. In all five plastra of *T. tedwhitei* the pectoral-humeral sulcus is separated from the entoplastron by a distance equivalent to about 1/2 to 1/3 the median length of the pectoral scute itself. In *T. osborniana* and its relatives the entoplastron tends to be very close to or in contact with the pectoral-humeral boundary in spite of the extreme narrowing of the pectoral scute. In *T. brontops* and *T. amphithorax* of the Oligocene the entoplastron is also in contact with the pectoral-humeral boundary, but that is less surprising here since the pectoral scute is quite large. The difference which *T. tedwhitei* manifests in this respect from the other Miocene and the Oligocene species is not great and may probably be bridged by individual variation when more specimens are known. It does, however, seem to indicate a trend in *T. tedwhitei* different from that in *T. osborniana,* etc. With regard to this character, *T. sellardsi* and *T. tedwhitei* are quite in agreement.

3. The entoplastron cannot be accurately measured in *T. tedwhitei* except in the type and in plastron 5. In the type, the width of the entoplastron is 71 mm., its length 67 mm.; the same values in plastron 5 are 67 mm. and 59 mm. respectively. The entoplastral length is thus about 9/10 its width. In *T. osborniana* and in the closely similar forms of the Miocene and Pliocene, the length was about 3/4 the width, as it was also in the Oligocene *T. brontops. T. amphithorax,* on the other hand, departs in the other direction from the condition of *T. tedwhitei,* having the entoplastron slightly longer than wide (104 mm. wide, 108 mm. long, Hay 1908). According to Loomis' figure the length of the entoplastron in *T. sellardsi* must have been about 9/10 its width, as in *T. tedwhitei.*

4. Four of five plastra[2] of *T. tedwhitei* show the gular region scarcely distinct from the general contour of the anterior lobe. The same region is somewhat more developed as a projecting gular prominence in *T.*

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[1] Loomis gives no measurements, but from his figure the pectoral-abdominal ratio must be between 1/12 and 1/15.

[2] In plastron 2 this area is missing.

osborniana and its group and much more developed in *T. arenivaga* of the Lower Miocene and in *T. brontops* of the Oligocene. Oligocene *T. amphithorax* and Eocene *T. uintensis*, on the other hand, have the gular prominence just as little distinct from the contour of the anterior lobe as in *T. tedwhitei*. This is equally true of *T. sellardsi*.

The striking similarity of the four plastra of *T. tedwhitei* in this as in other regards, permits much greater confidence in the use of these rather minor characters *in this group* than would otherwise be at all possible. The nearly identical differentiation of the gular region (at least in ventral view) in these four specimens is in strong contrast with the situation in *Gopherus* and in *Chelonoidis* in which individual and sexual differences in this region can be very great.

5. The dorsal aspect of the gular region, in the four specimens of *T. tedwhitei* in which this region is known, presents some interesting differences in the anteroposterior length of the swollen area and the degree of excavation of its caudal margin. The length of this "epiplastral lip" and the degree of excavation are directly correlated and, in three of the plastra, (the type and plastra 3 and 4) there is a consistent increase in both characters with size. In plastron 5, however, though it is larger than the type, both the dorsal length of the lip and the amount of posterior excavation are less, so that this region is less differentiated than in any of the other plastra. The dorsoventral thickness of the lip again varies directly as the dorsal length.

6. The inguinal scute in *T. tedwhitei* was apparently large and reached the femoral. It is satisfactorily discernible only on the left side of the type, but the partial sulci present in other specimens seem consistent with this description. A large inguinal scute is apparently characteristic of *Hesperotestudo*. A small scute is figured by Hay (1908) for *T. amphithorax*, but I have been unable to verify this on the type material at the American Museum. A small inguinal, not reaching the femoral, seems to be very characteristic of *Stylemys nebrascensis*, according to the many specimens I have examined. In Recent forms this character seems to be sufficiently constant to help in discriminating species groups; it may assist also with fossil forms.

7. The xiphiplastral notch is distinct and angular but not deep in the four plastra or partial plastra of *T. tedwhitei* in which it is preserved. In contrast, it is less distinct, wide and very shallow in *T. osborniana* and its close relatives. In both *T. brontops* and *T. amphithorax* the notch is very like that in *T. tedwhitei*. Loomis (1927)

specially commented on the distinctness of the notch in *T. sellardsi;* as he figures it, it is, indeed, very similar to that in *T. tedwhitei.*

8. With regard to the characters of the carapace we are not as fortunate as with those of the plastron, since we have only one carapace which is even approximately complete. From this, however, we may frame a rough estimate of the size and shape of the shell. The length of the carapace may be estimated as about 370 mm., the width as approximately 300 mm.; it was therefore about 4/5 as wide as long and distinctly parallel-sided, not globular. The sides were quite vertical, and the height may have been in the neighborhood of 150 mm.

In its parallel-sided contour *T. tedwhitei* was like *T. sellardsi* and rather unlike *T. osborniana* and its relatives which tend to a more nearly hemispherical carapace shape.

9. The anterolateral corners of the carapace flare above the limbs in *T. tedwhitei,* but between these flared corners, the anterior margin is essentially straight. This condition is rather characteristic of the whole assemblage which I called *Hesperotestudo* in my 1950 paper. The general impression is one of an indentation of the anterior margin, but this is not due to a real notch at the nuchal region as in some other turtles but solely to the considerable flare of the anterolateral margins.

10. The nuchal scute is preserved in three specimens in *T. tedwhitei.* In the more complete carapace it is about twice as long as wide, but in the other two instances it is significantly broader, though still longer than wide. This is another feature in which it is in general agreement with the members of the broad group *Hesperotestudo. T. sellardsi,* on the other hand, was described by Loomis (1927) on the basis of the Amherst specimen as having a very small nuchal which did not reach the anterior margin. Material referred to *T. sellardsi* at the M.C.Z. shows this scute to be of more normal *Hesperotestudo*-like character, longer than broad and reaching the anterior shell margin.

11. The vertebrals and neurals, so far as known, are essentially as in the other members of *Hesperotestudo* in which they are known. Vertebral 1 is very broad but does not reach, by a considerable interval, the second marginal of either side. Vertebral 4 is not completely known but was evidently longer than wide. Neurals 2 and 4 are octagonal (seen in two specimens). The first neural is elongate, oval in the usual fashion; neurals 3 and 5 are quadrilateral; neurals 6, 7 and 8 are hexagonal, short-sided in front.

12. The suprapygals are not distinctive; the pygal is rather narrow and bowed outward as in Loomis' figure of *Testudo sellardsi.*

13. The pleurals in *T. tedwhitei* are quite primitive in not displaying any trace of the alternate widening and narrowing of their distal ends, a feature characteristic of most advanced tortoises and seen well-developed in *T. osborniana* and *T. orthopygia,* but scarcely developed in *T. brontops* and not present in *T. amphithorax, T. impensa* and *T. sellardsi.*

14. The costo-vertebral sulci in *T. tedwhitei* are distinct but not deep, by no means so incised as sometimes in *T. sellardsi.* The latter, however, is a giant form, and this feature of deeply incised sulci may be suspected to be correlated with its great size. The other *Hesperotestudo* which are sufficiently known, none of quite comparable size, never show this deeply incised condition of the scute boundaries. The anterior and posterior margins are also more reverted in *T. sellardsi* than in the other forms.

15. A humerus and a small femur, both of normal testudine character, are referred to *T. tedwhitei.* The humerus has a slender rounded shaft without notable compression in any plane and with only a roughened area of attachment for the latissimus dorsi, not a pit. The femur, on the other hand, like that of *T. osborniana,* has the shaft compressed in the plane of the head and hence the shaft is rather quadrate in section.

Phyletic Relationships

The diagnosis above of *T. tedwhitei* has explicitly compared the new species with *T. sellardsi* as described from a specimen at Amherst, by Loomis (1927). I have made this special comparison because I want to evade, in the present discussion, the issue of the identity of the *Testudo sellardsi* of Loomis, described from a complete shell from Melbourne, Florida, with *Testudo sellardsi* Hay, the type of which is a xiphiplastron from Vero, Florida. Loomis' equating of his form with that of Hay may or may not be correct, but that point is not germane in the present instance.[1]

If now we compare *Testudo sellardsi,* as so defined, with *T. osborniana,* the type species of *Hesperotestudo,* certain differences are

[1] I feel it necessary to deprecate the description by anyone, even by one so experienced as Hay, of a new species of tortoise from material as poor as the type of *T. sellardsi.* Especially is it unfortunate that Hay described two species of giant tortoise from Vero from different parts of the shell!

evident. These differences, however, are not major ones. It would seem initially probable that they are merely specific and not group differences, since they are outweighed by the resemblances held in common between *T. sellardsi* and *T. osborniana,* and which separate them very clearly indeed from the species of *Gopherus.*

It therefore seemed logical, in 1950, to infer the descent of the Florida giant tortoise from *T. osborniana* or *T. osborniana*-like ancestors. But the discovery of *T. tedwhitei* changes this picture radically. It is obviously, in view of its many special resemblances, a much more suitable Miocene ancestor of the Pleistocene giant than *T. osborniana* or its close relatives. So with the entrance of *T. tedwhitei* into the picture, we see not one but two phyletic lines within *Testudo* in North America, separate at least since the Lower Miocene.

It is now desirable to set down as a first approximation the features which seem to distinguish these two phyletic lines.

Thus, the *T. tedwhitei* lineage appears to differ from the *T. osborniana* series by having:

(1) the carapace parallel-sided rather than rounded;

(2) the xiphiplastral notch distinct and angular rather than indistinct and rounded;

(3) the pectoral scute appreciably posterior to the entoplastron rather than in contact with it;

(4) the entoplastron about as wide as long rather than noticeably wider than long;

(5) the gular region less differentiated;

(6) the pectoral scute less narrowed.

None of these differences can be conceived of as an absolute difference. We are dealing not with *key* differences but with assemblages of characters that, in my judgment, empirically set apart two groups of species.

These two groups of species are indicated as closely related because of the common possession of the following characters:

1. a nuchal scute longer than wide;
2. a pectoral scute tending (with time) to become more and more narrowed;
3. an elongate fourth vertebral scute;
4. a differentiated neural sequence early acquired (in the time series);
5. markedly flared anterolateral and posterolateral margins;

6. a more convex shell than that of compared forms.

In the *T. osborniana* series in which alone skulls associated with shells are known, the characters listed above are associated with distinctive features of the premaxillary alveolar surface (a pit without a median ridge) and of the external surface of the dentary (fine vertical ribbing). These skull characters are assumed to hold for the *T. tedwhitei* series also.

In thus assuming two closely related parallel series we have two potential sources of confusion. (1) In later members of the two series, parallel variation may make closer the resemblance of forms which were distinct over a long period. Especially is this probable if, as in the present case, there appear to be similar trends with time (as in the narrowing of the pectoral scute) but trends pursued at different rates in the two series. Reversal of evolutionary trend is also a possibility. (2) The earlier members of the two series, as they approach in time their common ancestor, should be progressively less and less distinct one from the other.

Some instances of the first possibility of confusion may be expected to turn up as knowledge of Tertiary and Quaternary tortoises increases. The other point we may consider at this time in terms of the known Oligocene and Eocene tortoises.

In the Oligocene two very distinct species of *Testudo* have been described: *T. brontops* and *T. amphithorax*. On the character of the gular region, *T. brontops* with this region highly differentiated belongs with the *T. osborniana* series, and *T. amphithorax* with the same region not at all distinct, belongs with the *T. tedwhitei* series. The width-length ratio of the entoplastron arranges the two species in the same way. The pectoral scutes in both are very much wider than in Miocene forms, but in *T. brontops* the ratio of pectoral length to abdominal length is somewhat less than 1/4, in *T. amphithorax* somewhat more than 1/4, possibly an indication that the trend to greater narrowing of the pectoral was present in *T. brontops* to a somewhat greater degree than in *T. amphithorax*. This again would be consistent with a position of *T. brontops* in the *T. osborniana* line, *T. amphithorax* in the *T. tedwhitei* line. On the other hand, in certain other characters on which it is possible to distinguish the Miocene forms, no distinction is possible in the case of the Oligocene forms. In both species the pectoral-humeral sulcus is in contact with the lower margin of the entoplastron; in both the xiphiplastral notch is distinct and angular. *T.*

brontops had the carapace parallel-sided though possessing a wide shell; the shell of *T. amphithorax*, though not completely known, was probably narrower but also parallel-sided.

In the Eocene, only *T. uintensis* Gilmore has previously been referred to the genus *Testudo*. In that form the gular region is not more differentiated than in *T. amphithorax* or *T. tedwhitei*; it should therefore belong to that series. The entoplastron is about as wide as long in the unique specimen of the species; this also might count it as a member of the *T. tedwhitei* series. On the other hand, the carapace has a rounded rather than a parallel-sided contour; this might place it in the *T. osborniana* series. In still other respects it is much more primitive than any of the forms previously cited. The pectoral scute is about half the abdominal scute in length. The supracaudal scute is divided as in emydines or *Hadrianus*.

If *T. uintensis* is placed as a member of the *T. tedwhitei* series on the basis of the absence of gular differentiation, it will be to species referred to "*Hadrianus*" that we will have to look for the antecedent to the *T. brontops* — *T. osborniana* series. All so-called *Hadrianus* have a gular prominence well differentiated; this is true even of the Wasatch species. All are otherwise very primitive and differ from the forms called "*Testudo*" only in their primitiveness. Their supposed generic separation is no ground for doubting their ancestral relation to the later forms called "*Testudo*." Rather it is preferable to regard the generic distinction as invalid or at best of subgeneric value. "*Hadrianus*" *corsoni* is in most respects primitive enough to have given rise to any of the later *Testudo* of the Western Hemisphere.

In one respect only is there a difficulty and that not an important one. All the "species" called *Hadrianus* have rather parallel-sided shells combined with a differentiated gular region. *T. uintensis* has an undifferentiated gular region combined with a rather rounded shell. This is quite the reverse of the character combination we found to be present in Miocene and later species. In the Oligocene we have seen that both the assignable species have parallel-sided shells. Presumably this means only that the shell contour character, *if valid at all*, was not firmly fastened on either series until the Miocene.

This mixture and merging of the characters of the two series in the Eocene is indeed what we should expect. The series which are quite distinct in the Miocene, appear more closely approximated in the Oligocene and merge in the Eocene.

With the clearer view which the concept of two lineages within *Hesperotestudo* gives us, let us look now at certain previously problematical Miocene species. These forms poorly understood till now fall into place.

T. ducatelli Collins and Lynn (Hemingfordian Miocene of Maryland) is a form with the gular region of the plastron not distinct from the contour of the anterior lobe, the entoplastron very slightly wider than long, pectoral scute about 1/5 the abdominal in median length and touching the entoplastron on one side of the unique specimen, inguinal scute large, reaching femoral, xiphiplastral notch well-marked but not deep. The carapace except for the octagonal second neural and a few peripherals and partial pleurals is unknown. I placed this (1950, pp. 27-28), with some misgiving, as possibly a *Gopherus*, but with the new information now available I place it with much more confidence as a relative of *T. tedwhitei*.

T. farri Hay (Barstovian Miocene of Montana) is known from most of a crushed shell. The nuchal scute is longer than wide. The anterolateral corners of the carapace are not preserved. The second and fourth neurals are octagonal. The pleurals are alternately narrowed and widened distally. The gular region is not distinct from the contour of the anterior lobe. The entoplastron is just as wide as long. The pectoral scute, its anterior margin very close to but not touching the entoplastron, is about 1/7 the abdominal in median length. The xiphiplastral notch is distinct but not deep. This species, even more certainly than *T. ducatelli*, is a relative of *T. tedwhitei*.

With the addition of these forms the record of the twin lineages within *Hesperotestudo* becomes much more nearly complete, and the formerly obscured evolutionary picture is in part at least resolved into clearly defined elements. A few difficulties, however, remain:

(1) The discovery of the two lineages within *Hesperotestudo* forbids us to assign to either one of them the form *Testudo gilberti* Hay, known only from a skull. I am quite uncertain of the value of the differences described by Hay between the skulls of *T. gilberti*, *T. impensa*, *T. osborniana*, and *T. orthopygia*, and I do not think this problem will be amenable to solution until we have still more skulls *associated* with shells.

(2) There is a problem also in the allocation of *Testudo crassiscutata* Leidy of the Florida (Peace Creek) Pleistocene. In this form, unfortunately incompletely known, the anterior plastral lobe is much as in the

T. tedwhitei series, but the xiphiplastral notch is as shallow as in the *T. osborniana* series. This species may, perhaps, be provisionally placed in the *T. tedwhitei* series, but it cannot be pretended that this rather arbitrary placement implies that the situation is understood. What is the relationship of this giant form to *T. sellardsi*? What are Pliocene *T. louisekressmani* Wark and *T. hayi* Sellards and Pleistocene *T. luciae* Hay? Were there both giant *Testudo* and giant *Gopherus* in the Florida Pleistocene? The scattered remains are tantalizing and the problems of nomenclature frustrating. Furthermore, in addition to the puzzling Florida giants there are the giant thick shelled forms of the Ashley River beds of South Carolina, in regard to which Leidy's name *Eupachemys obtusus* based on a single peripheral must be considered. This latter may possibly represent a late member of the series of which *T. tedwhitei* is now the best known example.

(3) An unfortunate nomenclatorial tangle exists. I have traced two lines of what I previously called *Hesperotestudo* back to the base of the Oligocene. If, as seems entirely probable, these two lines find their common ancestor in the earlier Eocene in some species of what has been called "*Hadrianus*", then according to modern concepts it is impossible to retain these two lineages in *Testudo*, if *Hadrianus* is accepted as a full genus. However, as I have indicated and as Gilmore had already suggested in 1915, *Hadrianus* is very imperfectly defined as against the genus *Testudo* broadly conceived. Its characters may be matched elsewhere in that genus, and it is impossible to retain the name at all unless as a subgenus. If then *Hadrianus* is regarded as a subgenus, that will obviate the major difficulty, and that solution is proposed here.

This will not, however, solve all our problems. If the apparently plausible hypothesis of the separate descent of our two lineages from forms called *Hadrianus* is true, either *Hadrianus*, as the oldest available name, must be used as the inclusive subgenus name of all North American *Testudo* (it then becomes undefinable), or alternatively a new subgenus name is required for the line of which *T. tedwhitei* is a central member. In the latter case, probably but not certainly, Leidy's name *Eupachemys* is available.

Fortunately, failure to solve this problem at this time involves no serious difficulty since all the forms concerned belong quite certainly to the genus *Testudo*.

Figure 1 presents diagrammatically the relationships as I now see them of the determinable members of North American *Testudo.*

Faunal Associations of the New Species

In addition to the excellent tortoise material which forms the hypodigm of *T. tedwhitei* there are a few additional turtle fragments which can be assigned with fair certainty to the pond turtle genus *Pseudemys* but which cannot be more precisely placed. The fragments in question (Plate 4) are one complete (unillustrated) and two partial nuchal plates, a single complete pleural, a left xiphiplastron and a left epiplastron. The delicacy of the surface sculpturing plus the greater resemblance in some minor details to individual members of the *Pseudemys floridana* group probably imply that the fragments belong to some extinct member of that group, but in the absence of more material and particularly more comparative material it is quite useless to further discuss these remains at this time.

Conspicuously absent from the preserved testudinate fauna of the Miocene of Thomas Farm are trionychids and chelydrids which are very important in the fauna of Florida today and which certainly were abundant also in the Pleistocene faunas (as considerable material at the M.C.Z. proves).

This comparative rarity of aquatic types (the absence, indeed, so far as the present record shows, of two very important aquatic turtle families) probably points as does the mammalian record (the predominance of horses, etc., Romer, 1948) to an ecology for the Miocene of Florida very different from that now characteristic of the area. "It was then, as now, a low country — but a low plain, relatively dry and grass-covered — a prairie in the western rather than the floridian sense of that term" (Romer, 1948, p. 10). The amphibian fauna recently described by Tihen (1951) would appear to point in the same direction — most abundant a species of *Bufo,* less frequent a *Rana.*

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REFERENCES

Collins, R. L. and W. G. Lynn

1936. Fossil turtles from Maryland. Proc. Amer. Phil. Soc., vol. 76, pp. 151–173.

Gilmore, C. W.

1915. The fossil turtles of the Uinta formation. Mem. Carnegie Mus., vol. 7, pp. 101–161.

Hay, O. P.

1908. Fossil turtles of North America. Carnegie Institution of Washington. Publication No. 75, 568 pp.

1916. Description of some Floridian fossil vertebrates belonging mostly to the Pleistocene. Rept. Florida Geol. Surv., vol. 8, pp. 41–76.

Loomis, F. B.

1927. A giant tortoise from Florida. Amer. Jour. Sci., ser. 5, vol. 13, pp. 435–439.

Romer, A. S.

1948. The fossil mammals of Thomas Farm, Gilchrist County, Florida. Quart. Jour. Florida Acad. Sci., vol. 10, pp. 1–11.

Tihen, J. A.

1951. Anuran remains from the Miocene of Florida with the description of a new species of *Bufo*. Copeia, 1951, pp. 230–235.

Williams, E. E.

1950. *Testudo cubensis* and the evolution of Western Hemisphere tortoises. Bull. Amer. Mus. Nat. Hist., vol. 95, pp. 7–36.

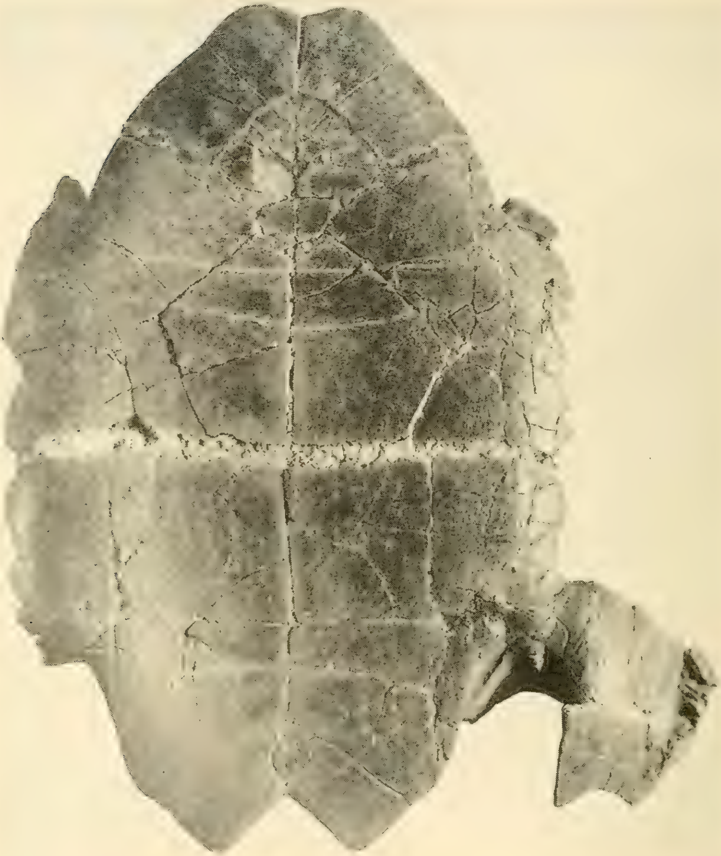

Plate 1. *Testudo tedwhitei* new species, ventral view of type plastron. x$\frac{1}{3}$.

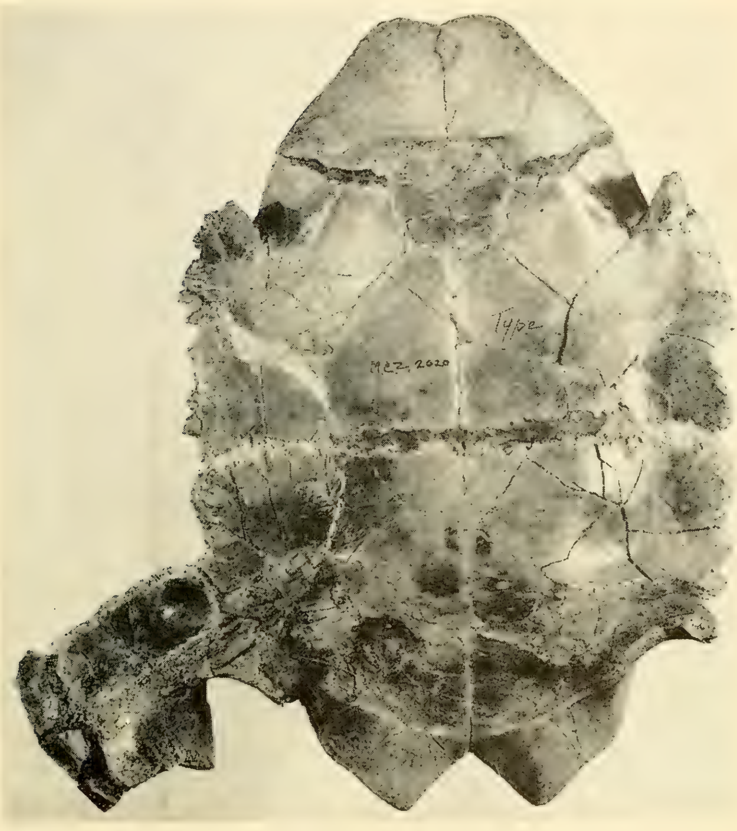
Type
MCZ 2020

Plate 2. *Testudo tedwhitei* new species, dorsal view of type plastron. x1/3

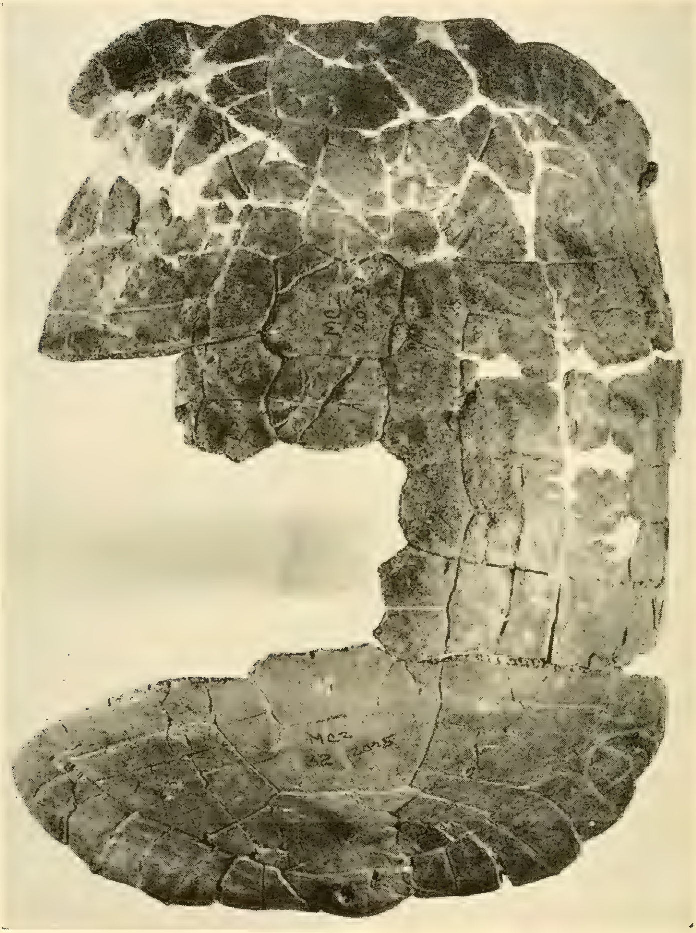

Plate 3. *Testudo tedwhitei* new species, referred carapace. x about ⅓.

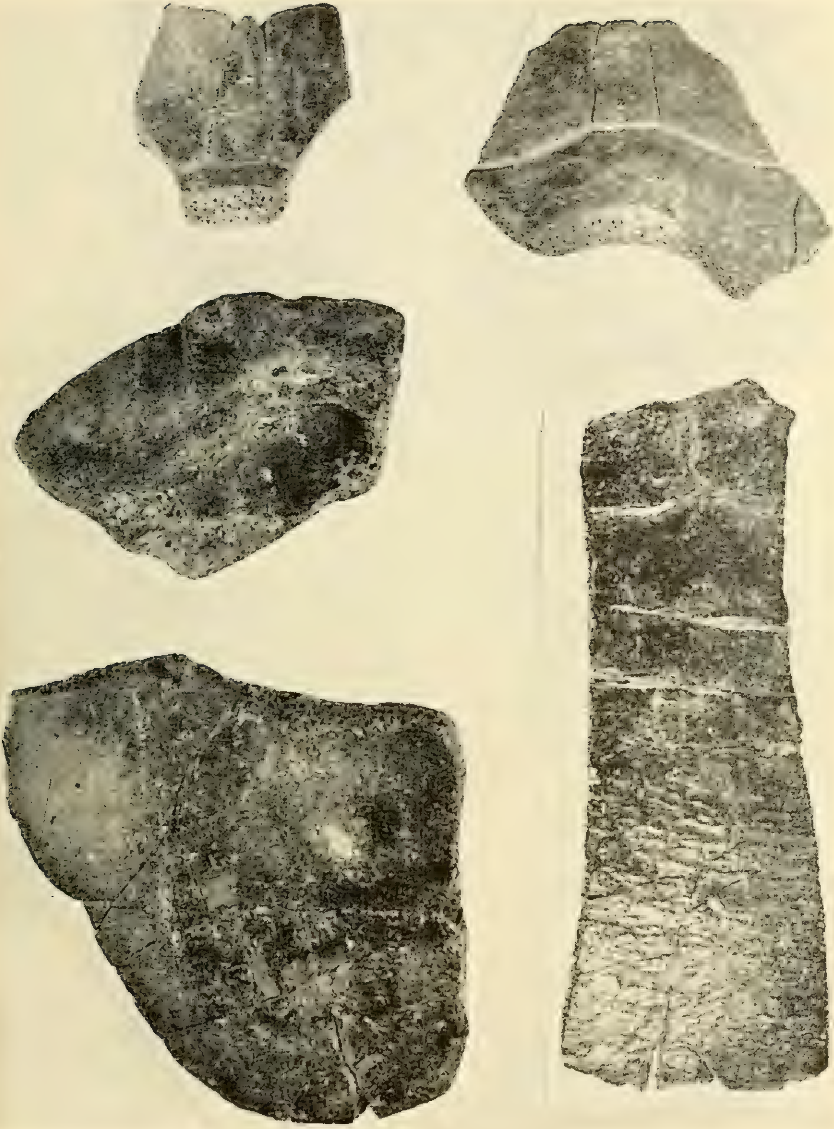

Plate 4 *Pseudemys* sp., various fragments from the Thomas Farm Miocene. x 1.

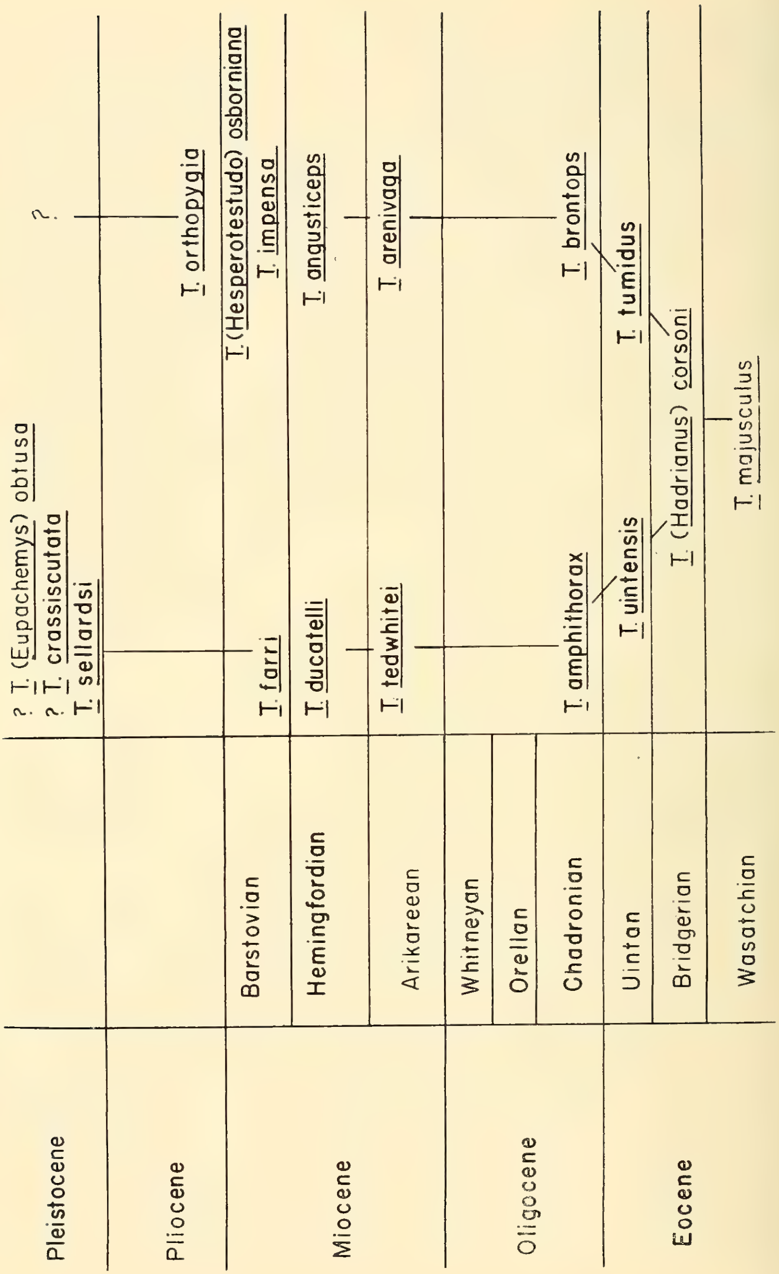
Pleistocene
Pliocene
Miocene
Oligocene
Eocene
Barstovian
Hemingfordian
Arikareean
Whitneyan
Orellan
Chadronian
Uintan
Bridgerian
Wasatchian
? T. (Eupachemys) obtusa
? T. crassiscutata
T. sellardsi
?
T. orthopygia
T. (Hesperotestudo) osborniana
T. impensa
T. farri
T. ducatelli
T. angusticeps
T. tedwhitei
T. arenivaga
T. amphithorax
T. brontops
T. uintensis
T. tumidus
T. (Hadrianus) corsoni
T. majusculus

Fig. 1. Diagram of presumed phyletic relationships of North American *Testudo* species.

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